# Rhodora

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# The New England Botanical Club, Inc.

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*Agalinis acuta* Pennell (Sand-Plain Gerardia). A very rare plant of the coastal plain in danger of extinction; known only from Cape Cod and Long Island. Recently listed by the U.S. Fish & Wildlife as Threatened. Original artwork by Tess Feltes; from *New England's Rare, Threatened and Endangered Plants.* Crow, G.

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# Rhodora

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SYMPOSIUM PROCEEDINGS

# PLANT CONSERVATION: A BIOGEOGRAPHICAL PERSPECTIVE

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RHODORA, Vol. 91, No. 865, pp. 3–5, 1989

# PLANT CONSERVATION: A BIOGEOGRAPHIC PERSPECTIVE

## FOREWORD

LESLIE J. MEHRHOFF
Symposium Committee Chairman

"My plea is for wholehearted protection of that helpless but tremendously interesting group which may be called the fugitive aristocrats, the completely isolated and usually entirely overlooked small colonies, doing no one any harm, but of utmost importance to the student of life and its history through the last 100,000,000 years."
M. L. Fernald (1939)

Fernald's "fugitive aristocrats" are the rare species, those of biogeographic significance, with which this symposium issue of *Rhodora* is concerned. Conservation of our native flora has always been a concern of the New England Botanical Club. Merritt Lyndon Fernald was, along with many of the first members of the Club, actively involved with the preservation of rare native plant species.

In keeping with this tradition of concern, the Council of the New England Botanical Club approved, in late 1986, a second symposium focusing on plant conservation. The first, entitled Rare and Endangered Plant Species in New England, was held almost a decade earlier. The inspiration for this symposium came after I attended the National Forum on Biodiversity held in Washington, DC, in September, 1986. I mentioned the idea of a second New England Botanical Club symposium to then Club President Rolla M. Tryon, and to him goes credit for the inclusion of biogeography as the central theme around which emphasis on plant conservation could revolve.

With the Council's blessing a committee consisting of then Club Vice-President Garrett E. Crow and Council members Julie A. Hambrook, W. Donald Hudson, Jr., and Bruce E. Sorrie was selected to help organize the 1988 New England Botanical Club's symposium entitled, "Plant Conservation: A Biogeographic Perspective."

We enthusiastically undertook the charge and began planning early in 1987. There was much more to do than we anticipated and it was good that we had the positive experience of the 1979 NEBC Symposium on which to rely. The idea was to have the

morning session give an historic perspective, move through the fossil record of the northeastern flora, and then discuss current plant distribution. Speakers were chosen whose research would address these goals.

The Council allowed the Distinguished Speaker meeting to be changed from its usual April date to coincide with our May symposium. This change, in effect, gave us an additional keynote speaker. Dr. Hugh H. Iltis of the University of Wisconsin did a splendid job of setting both the mood for the following day's symposium and for raising many questions on plant conservation and current theories with which he disagrees on the extensive frigidity of the South during the Pleistocene. Saturday morning's keynote address by Dr. Robert F. Thorne of Rancho Santa Ana Botanic Garden gave those in attendance a phylogenetic perspective to biogeographic concerns.

Morning speakers laid a regional groundwork by presenting paleobotanic data and current floristic information. In the afternoon, representatives of each of the New England states were given opportunity to update plant conservation efforts in their respective states since the last symposium. Specific research on taxa of biogeographic interest concluded the afternoon session. Past President Rolla Tryon of Harvard University eloquently summarized the presentations and charged us with a continued need for investigations and for preservation of those biogeographically interesting species to which Fernald referred as the "fugitive aristocrats."

Four papers presented at the symposium are not presented here. Because of the number of slides (two simultaneous projectors—manually operated!), the presentation of Hugh Iltis does not lend itself well to this medium. Arthur Cronquist's work is well known and he felt it adequately covered in his many works on this subject. Cathy Paris's data have recently been published elsewhere (Systematic Botany 12: 240–255, 1988) and she did not want to duplicate this paper. Susan Gawler's full remarks will appear elsewhere as part of her thesis. Abstracts for the last three items have been included.

The Council of the New England Botanical Club generously chose to underwrite the cost of this symposium in the face of shrinking financial support. Additional support came from the Chewonki Foundation, Wiscasset, Maine, The Connecticut Geological and Natural History Survey, Connecticut Department of

Environmental Protection, and the U.S. Fish and Wildlife Service. Josephine W. Ewing did the announcement design and layout. Megan Rollins and Yolanda Aspland helped with the typing. The map of New England was used with the permission of C. Barre Hellquist. Nancy Eyster-Smith videotaped the entire symposium. Copies of these tapes may be borrowed from the NEBC library. David S. Barrington took able charge of refreshments for the entire symposium.

On behalf of the Symposium committee, I would like to thank all those who helped make the 1988 New England Botanical Club symposium on Plant Conservation: A Biogeographic Perspective a resounding success. To those of us in the plant conservation field our path should be more clearly illuminated by the many insightful presentations and beneficial discussions. Fernald (1939) also gave us direction in his article entitled, "The problem of conserving rare native plants," when he said, "True conservation leaves nature, mother of us all, uninjured and the true conservationist is a lover and defender of uninjured nature."

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# PLANT CONSERVATION: A BIOGEOGRAPHIC PERSPECTIVE

## INTRODUCTION

GARRETT E. CROW
President, NEBC

I am extremely pleased to be able to welcome you to the New England Botanical Club's second symposium, "Plant Conservation: a Biogeographic Perspective." As many of you will recall, nine years ago, on May 4–5, 1979, the New England Botanical Club sponsored an important symposium at Harvard University which focused on New England's rare and endangered plants. The two-day symposium addressed issues concerning 1) biology of endangered species, 2) plant conservation concerns in the New England states, and 3) conserving rare plants and their habitats. The proceedings of the symposium were published in the January, 1980 issue of *Rhodora* (Vol. 82, No. 829).

That symposium brought into focus a great deal of work on the flora of New England which had been stimulated by the then recent passage of the Endangered Species Act. Congress officially recognized the issue of endangered species in 1973 by declaring in the Act that ". . . various species of fish, wildlife, and plants in the United States have been rendered extinct as a consequence of economic growth and development untempered by adequate concern and conservation . . ." and that others ". . . have been so depleted in numbers that they are in danger of or threatened with extinction. . . ." Although we fully recognize that natural events may contribute to the demise of a given species, this declaration by Congress unfortunately applies all too well to the biota of New England. Industrial, residential, and recreational development in our region has placed great demands on our environment and the rapid growth of our region continues to have a major impact on the existence and character of our flora.

The New England Botanical Club has had from its very first meeting a very great concern for the flora of the region. On December 10, 1895 a meeting of gentlemen interested in Botany, and especially the Flora of New England, met at Dr. W. J. Farlow's house in Cambridge (next door to the building that today houses the Harvard University Faculty Club). Initially the scope of the Club's activities was to cover the local flora of Massachusetts (the

Berkshires seemed rather distant in those days) and the flora of the White Mountains of New Hampshire. The local effort began with a determination of the flora of the Metropolitan Park Reservations, and a sum of $200 was provided by the Park Commission for the mounting and processing of "worthy specimens" to be placed in the Club's newly initiated herbarium. A room in the Agassiz Museum was kindly placed at the disposal of the Club by the President of Harvard University, an offer which the Club gratefully accepted. The NEBC soon established a botanical journal to distribute contributions to our knowledge of the flora of New England, as well as taxonomy and phytogeography in general, and much information has been dispersed in the pages of the 90 volumes of the Club's journal *Rhodora*. The NEBC herbarium has grown to house ca. 250,000 specimens of plants from New England.

We could hardly have a symposium focusing on biogeography without mentioning Professor M. L. Fernald. Although not a charter member of the New England Botanical Club, Fernald (at age 22) was among the first to be elected to membership in the newly established club. M. L. Fernald was clearly a predominant figure, contributing a great deal to our knowledge of the flora and phytogeography of the northeast. In fact, his hypothesis on persistence of plants in refugia of Gaspé is a central question in the theme of one of the papers being presented this afternoon.

The recent efforts by the Club to witness issues of plant conservation came with the establishment of the Natural Areas Criteria Committee in 1971. The committee, chaired by William D. Countryman, prepared a report for the New England Natural Resources Center entitled "Guidelines and Criteria for the Evaluation of Natural Areas" (Countryman et al., 1972, 1981). The report provided 1) a listing of categories of rare and endangered species of vascular plants, and 2) a listing of the physiographic categories of important natural areas in New England.

The New England Botanical Club established the Endangered Species Committee in 1977 and set as its goal the preparation and publication of coordinated lists of the rare, threatened, and endangered indigenous vascular plant species of the six New England states. In the fall of 1978, under the encouragement of Mr. Richard Dyer, and financial support of the U.S. Fish and Wildlife Service, these individual state reports were published: Maine (Eastman, 1978), New Hampshire (Storks and Crow, 1978), Ver-

mont (Countryman, 1978), Massachusetts (Coddington and Field, 1978), Rhode Island (Church and Champlin, 1978), and Connecticut (Mehrhoff, 1978) and were published by the U.S. Fish and Wildlife Service's Office of Endangered Species.

The Club's Endangered Species Committee next focused its attention on the development of a regional list and in April, 1981 published a list of 479 rare plant taxa pertaining to the entire New England region, including only taxa significant to all of New England (Crow et al., 1981). In collaboration with members of the Committee, Crow (1982) published *New England's Rare, Threatened, and Endangered Plants,* focusing attention on and providing a more comprehensive assessment of 101 of the rarest plants in New England. At that time two of the 101 taxa, the Furbish Lousewort (*Pedicularis furbishiae*) and Robbins' Cinquefoil (*Potentilla robbinsiana,* had been listed under the Endangered Species Act. Two more taxa, Small Whorled Pogonia (*Isotria medeoloides*) and Silverling (*Paronychia argyrocoma* var. *albimontana*), had been formally proposed for listing; the former taxon since has been formally listed and the latter has been withdrawn from the listing process.

In the nine-year interval since our last symposium, a great amount of research energy has been expended on endangered species in the New England region. It is then the purpose of this symposium to focus on what we have learned and the present status of New England's rare flora, and to place it all in a biogeographic perspective.

It is my privilege to introduce to you our keynote speaker, Dr. Robert Thorne. Dr. Thorne is especially well-known for his writings relating to guiding principles of angiosperm phylogeny and for Thorne's "phylogenetic shrub," a phylogenetic classification of the Angiospermae. But you may be surprised to learn that although Bob Thorne has long been associated with the Rancho Santa Ana Botanic Garden in California, his undergraduate days were spent on the campus of Dartmouth College where the late Dr. James Poole (a long-time member of NEBC) was his professor in botany. His master's degree involved aquatic plants under W. C. Muenscher at Cornell University. In fact, he still gets his feet wet, with his continued interest in the flora of the vernal pools which develop each spring in southern California. Dr. Thorne will speak to us on the topic "Angiosperm Phylogeny and Geography."

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# PHYLOGENY AND PHYTOGEOGRAPHY

ROBERT F. THORNE

## ABSTRACT

Biogeography is a useful tool for the phylogenist. Distribution patterns, past and present, can be most instructive in indicating possible relationships. This observation is true because the closest living relatives of a phyletically unplaced taxon are more likely than not to be found in the same or adjacent areas rather than on distant continents. However, this generalization must be used with caution for many plant groups possess great vagility and have spread rapidly into appropriate habitats over the earth. The largely Old World Pittosporales are described in some detail as a prime example of application of this dictum of geographic plausibility. Archaic dicotyledons of the Australasian and Asian regions are discussed as other examples of the dictum, as are a few North American taxa such as *Simmondsia,* Crossosomataceae, and *Batis.* Additional angiosperms are listed without discussion for both North and South America.

Key Words: Phylogeny, phytogeography, geographic plausibility, Old World, New World

## INTRODUCTION

The two botanical disciplines of phylogeny and phytogeography are interdependent. Correct interpretation of one depends upon considerable knowledge of the other. Certainly in the study of distribution patterns and major disjunctions the plant geographer is heavily dependent upon accurate taxonomy and recognition of monophyletic genetic relationships. Incorrect determinations, mixed labels, and inadequate or inaccurate location data have led many a biogeographer astray. Likewise, the paleobotanist should have a good knowledge of the phylogenetic relationships and the past and present distribution of pertinent taxa to identify the plant fossils that are at hand.

Conversely, knowledge of the present and past distribution of a taxon and its presumed relatives can be critical in determining the phylogenetic relationships of that taxon. Generally the closest living relatives of a phyletically unplaced taxon are more likely than not to be found in the same or adjacent areas rather than on distant continents. This dictum should be used with caution for many plant groups possess great vagility and have spread rapidly into appropriate habitats over the earth's surface. This paper will present some examples of the application of this prin-

ciple, with especial reference to the Pittosporales (Thorne, 1975, 1976, 1977, 1981, 1983).

## PITTOSPORALES

The idea of geographic plausibility became part of my *modus operandi* more than a decade ago as I developed my concept of the Pittosporales (Thorne, 1975). As I was reconstructing what I regarded as natural orders, I had ejected as *taxa incertae sedis* a rather large number of families from many different generally accepted orders because the families obviously did not "fit" in those orders. A group of ten families from the Old World stood out because of their similar distribution patterns and their relatively primitive stem anatomy and floral morphology. Those ten families at that time were treated in five to seven relatively unrelated orders in each of four widely accepted systems of classification (Melchior, 1964; Cronquist, 1968; Takhtajan, 1969; Hutchinson, 1973) involving 16 different ordinal names. The most realistic treatment seemed to me to be that of Hutchinson (1973), with merely five different orders involved and seven families placed in the related Hamamelidales and Pittosporales. Since then I have added three more families to my concept of the Pittosporales.

At present in three current classifications (Cronquist, 1981; Dahlgren, 1983; Takhtajan, 1987) the 13 pittosporalean families are still treated in ten, eight, and 12 different orders, respectively. Obviously, my fellow phylogenists do not take into account phytogeographic plausibility in constructing their systems of classification. Conceivably my three suborders, Buxineae, Pittosporineae, and Brunineae, could be elevated into three related orders, Buxales, Pittosporales, and Bruniales, but I can see no need for further subdivision.

To examine this group of families graphically I drew up a chart of their characteristics. I was startled by the large number of salient features that they possessed in common beyond their geographic similarities. Among those characteristics members of my Pittosporales combine usually simple, exstipulate leaves; unspecialized xylem; radially symmetrical flowers with a definite number of stamens opposite the sepals; syncarpous gynoecium; often subapical, pendulous, anatropous ovules; and seeds with minute to linear embryo in abundant endosperm. The species display varied

habit, though most are small trees, shrubs, or twining undershrubs of relatively mesic habitats. They also share in common certain strong tendencies toward dioecism, apetalous or naked flowers, epigyny, crowding of small flowers into bracteate spikes or heads, porous anther dehiscence, and parietal placentation in monolocular ovaries.

**Buxineae**

Most primitive in their wood anatomy are the members of the Buxineae (or Buxales), including the archaic, widely distributed Buxaceae (the only family with some New World representation) (Carlquist, 1982) and monogeneric Didymeleaceae of Madagascar, Daphniphyllaceae of eastern Asia and Malesia, and Balanopaceae of Australasia. The primitive xylem of members of this suborder is distinguished by the very small, long to medium vessel elements, exclusively solitary and with 15- to 30-barred scalariform perforation plates, and very small, scalariform to opposite or transitional intervascular pitting; xylem parenchyma diffuse and apotracheal; rays markedly heterocellular, 2 to 4 cells wide with numerous uniseriates; and tracheids or fiber-tracheids, very short to moderately long, with large to small bordered pits. Except for some suffrutescent perennials or shrubs in the Buxaceae and some shrubs in the Daphniphyllaceae, most members of the Buxineae are small trees of tropical to warm temperate, mesic forests with evergreen, exstipulate, simple, pinnately-veined, mostly glabrous and entire leaves. The flowers are much more specialized than the xylem and rather reduced, being unisexual though often possessing nonfunctional staminodia or pistillodia. The species are either monoecious or dioecious. The flowers are apetalous or naked, in tight bracteate racemes or spikes. The sepals, when present, are imbricate and usually four in number. Stamens are usually four to six, rarely numerous or reduced to two, with large anthers dehiscing by longitudinal slits. The gynoecium is syncarpous, abortive in or absent from male flowers, with three or two carpels and locules (apparently reduced to one in *Didymeles* Thou.), each usually with two anatropous ovules, bitegmic and crassinucellar, pendulous from the apex of each locule. The fruit is a loculicidally dehiscent capsule or drupe, and the seeds usually have a straight, axile embryo in copious fleshy endosperm (much reduced in *Balanops* Baill. or entirely absent in *Didymeles*).

*Didymeles,* as also some Buxaceae, is reported to have encyclocytic stomata (stomata surrounded by a rosette of subsidiary cells) (Koehler, 1980). Koehler also stressed the palynological similarities of *Didymeles* with members of the Buxaceae. The stomata of *Daphniphyllum* Blume and *Balanops* are paracytic or laterocytic. The alternate, evergreen, leathery leaves of these two latter genera are commonly subverticillate at the ends of the branches much as in some species of Pittosporaceae. Unlike members of the Buxaceae but similar to some pittosporums, species of *Balanops* and *Daphniphyllum* have an ovary that is imperfectly septate into 4–2 locules (with placentation thus parietal). The four families of the Buxineae are readily separable with their own suites of distinctive features and specializations due to evolutionary divergence, but they do appear to form a monophyletic group with probable common Cretaceous ancestry.

**Pittosporineae**

The essentially Australasian Pittosporineae with the three families Pittosporaceae, Tremandraceae, and Byblidaceae retain the least specialized flowers but have the most specialized xylem in the order. The Pittosporaceae, with nine genera and about 200 species, are mostly restricted to Australasia except for the large genus *Pittosporum* Banks ex Soland. apud Gaertn., whose wide range (Thorne, 1973) from southern Africa and Macaronesia to Japan and Polynesia nearly encompasses the total range of the order with the exception of the New World species of Buxaceae. Members of the family have typically actinomorphic, bisexual, pentamerous flowers with biseriate perianth of usually distinct, imbricate parts, and superior ovary with 2–5 complete or incomplete locules and numerous ovules on axile or parietal placentae.

The xylem of many Pittosporaceae (Carlquist, 1981) has vessel elements with simple perforation plates and alternate, small intervascular pitting; sparse, paratracheal parenchyma; almost homocellular rays with few uniseriates, and moderately-short, septate libriform fibers with simple or vestigially bordered pits. At least one of the New Caledonian species of *Pittosporum, P. paniense* Guill., has more primitive xylem with scalariform pitting on the vessel elements. It is significant that New Caledonian species among others also have subverticillate foliage much like that of species of *Balanops* and *Daphniphyllum* (Carlquist, 1980; Huang,

1965), similar incomplete septation and parietal placentation in the pistils, and an unusual mode of crystal occurrence, with "ray cells subdivided into cells each of which bears a rhomboidal crystal." Similar crystals are also found in *Balanops,* Tremandraceae, Brunineae, and the Hamamelidaceae (Carlquist, 1977b, 1977c, 1980), with which the Pittosporales share both primitive evolutionary level of wood anatomy and common ancestry in the Rosanae (formerly Rosiflorae).

The Australian Tremandraceae and Byblidaceae (Carlquist, 1976b, 1977c) were accepted by Dahlgren (1983) as part of his Pittosporales but Cronquist (1981) and Takhtajan (1987) place the Tremandraceae in their Polygalales, presumably because of stem anatomical features and poricidally dehiscent stamens. Carlquist (1977c), however, found tremandraceous wood anatomy to be remarkably similar to that of the Pittosporaceae. Also poricidal stamens are found in all three families of Pittosporineae (along with many other Australian taxa pollinated by hover flies). These three families must be closely related and stem from common Australian ancestry.

**Brunineae**

A somewhat more diverse suborder are the Brunineae, a group of primarily South African mesic relicts of mountainous areas including Bruniaceae, *Geissoloma* Lindl. ex Kunth, *Grubbia* Endl., *Myrothamnus* Welw., and *Roridula* Burm. f., plus the aquatic *Hydrostachys* Thou., also of South Africa but ranging north into tropical Africa and Madagascar. Each of these listed genera form monotypic families, distinct enough to be placed in separate, widely unrelated orders by other phylogenists. Carlquist (1975, 1976a, 1976c, 1977a, 1977b, 1978a, 1978b) has, however, studied very thoroughly the wood anatomy and relationships of these taxa and found them to be very similar both in the archaic xylem features and in features unrelated to specialization level such as the subdivided ray cells with rhomboidal crystals (Bruniaceae, *Geissoloma,* and *Grubbia*), plus striking similarities in floral morphology, embryology, and palynology. *Roridula* and *Myrothamnus* species are somewhat less similar in wood anatomy as well as in growth habit although all these South African plants are mesic shrubs.

Most divergent are the species of *Hydrostachys,* peculiar pin-

natisect-leaved, tuberous-stemmed hydrophytes specialized for life in seasonal streams. Yet even these species share with *Myrothamnus* species, some also reaching Madagascar, leaves with dilated bases; imperfect, naked flowers each sessile in the axil of a bract in a tight spike; dioecism; syncarpous pistil with divergent styles; similar pollen grains united in tetrahedral tetrads; and fruit a many-seeded, small capsule. Surely these African–Malagasy taxa share enough characteristics to merit treatment in the same suborder or order. At the very least, they deserve the same careful, objective study of their morphology and relationships as given their stem anatomy by Carlquist, as cited above.

## STILBACEAE

Another pair of somewhat more specialized South African taxa that are illustrative of the doctrine of geographic plausibility are the Stilbaceae and the genus *Retzia* Thunb. Both taxa were long buried in other families, the stilboids in the Verbenaceae and *Retzia* in the Loganiaceae. Both groups consist of woody shrublets with narrow, verticillate, sclerophyllous leaves, and both are restricted to the Cape Region of the Republic of South Africa. They have startlingly similar xylem anatomy (Carlquist, 1986), pollen grains, and iridoid glucosides (Dahlgren et al., 1979), two of which, unedoside and stilbericoside, are found in both *Retzia* and *Stilbe* Bergius. These and other morphological similarities command treatment of these two groups in the same family, the conserved Stilbaceae, probably as distinct subfamilies, possibly most closely related to the Buddlejaceae of the Bignoniales.

## ARCHAIC ANGIOSPERMS

Southeastern Asia and adjacent Malesia and Australasia have an inordinately large number of relict angiosperms, especially in the two superorders Annonanae and Rosanae (including Hamamelidanae). This richness in relicts abounding in primitive characteristics had led to an argument among botanists as to whether the area is the center of origin of the Angiospermae or is merely a great natural museum, or refugium, where unspecialized angiosperms and other vascular plants have been able to survive great climatic changes and other catastrophic events. Our inadequate knowledge of the fossil record and of tectonic events when the

angiosperms evolved makes it impossible to determine at present the place of origin of the angiosperms. Also we know that the area in question was divided in Cretaceous time into two major and several minor tectonic plates and that the Australasian and southeastern Asiatic plates were widely distant from each other.

It is possible that some of the relicts in eastern Malesia and Australasia may have immigrated to those areas from southeastern Asia after the two great plates came together in the Miocene some 15 million years ago (Thorne, 1978a). Certainly southeastern Asia, Malesia, and Australasia have long been great natural refuges for archaic plants in their dissected, moist, habitat-rich mountainous areas and isolated archipelagos. Also like the Guayana and Brazilian highlands, Africa, Madagascar, and other areas, eastern Asia and Australia have independently been major centers of origin and evolution for the angiosperms.

## ANNONANAE (formerly ANNONIFLORAE)

Perhaps most characteristic of the Asiatic–Malesian–Australasian regions are the numerous members of the Annonanae (Thorne, 1974) in which I now include the orders Annonales, Nelumbonales, Paeoniales, and Berberidales. This rather large group of relatively unspecialized flowering plants contains, in my opinion, the most archaic and least specialized of all angiosperms.

### Winteraceae

Probably retaining the largest suite of primitive characteristics are the ancient Winteraceae (Thorne, 1972, 1978b) with their highly disjunct Gondwanaland distribution pattern and a fossil record reaching back into early Cretaceous time (Walker et al., 1983). Among their more primitive (plesiomorphic) features are their woody habit with leaves simple, alternate, pinnate-veined, entire, petiolate, glabrous, evergreen, and exstipulate, with paracytic stomata and rather primitive leaf architecture; entirely vesselless wood, long fusiform cambial initials and tracheids, heterogeneous rays, and diffuse xylem parenchyma; bisexual, actinomorphic flowers with poorly differentiated perianth parts and variable number of mostly separate, spirally arranged organs; undifferentiated broad microsporophylls with lateral to apical, protuberant microsporangia; pollen grains distally mono-aper-

turate; carpels styleless megasporophylls with partly free margins forming conspicuous double stigmatic crests; anatropous, crassinucellate, bitegmic ovules on marginal or submarginal placentae; and embryo rudimentary in abundant endosperm.

The Winteraceae have their great center of preservation, and perhaps development, in Australasia especially in the highlands of New Caledonia, that island treasurehouse of archaic relicts. Four of the eight currently accepted genera are well represented there, two of them endemic. A fifth genus is endemic to New Zealand and another to South and Central America from Fuegia and the Juan Fernandez Islands north to Mexico. A seventh was collected once in the rainforests of northern Madagascar, and an eighth is wide-ranging from Tasmania north to Borneo and the Philippines.

**Illiciineae**

The probable closest relatives to the Winterineae are the Illiciineae, with the two families Illiciaceae and Schisandraceae heavily developed in eastern Asia with a very few species of *Illicium* L. and *Schisandra* Michx. found also in southeastern North America, the former also reaching the Greater Antilles and eastern Mexico. More distantly related to the Winteraceae, but like them primitively vesselless, is the monospecific family Amborellaceae, restricted to New Caledonia.

**Austrobaileyineae and Annonineae**

Australasia, here broadly defined to include New Guinea, New Caledonia, Fiji, and New Zealand, also harbors another group of Annonalian relicts containing the monotypic Austrobaileyaceae of northern Queensland, intermediate between the Annonineae and Laurineae; the closely related monotypic Himantandraceae and ditypic Eupomatiaceae of eastern Australia and New Guinea, ditypic Degeneriaceae of Fiji, and relatively large, mostly Asiatic family Magnoliaceae, which overlaps the first two in the New Guinea highlands. As is true for the calycanthaceous *Idiospermum* S. T. Blake of northern Queensland, the Winteraceae, and three archaic genera of Hamamelidaceae, the closest relatives of these Australasian plants are in eastern Asia. All of the 12 generally accepted and mostly endemic genera of Magnoliaceae, most of

the Illicineae, the other two genera of Calycanthaceae, and most of the approximately 30 hamamelidaceous genera are represented in eastern Asia. If these relicts had not reached Australasia after the coming together of the Australasian and Asiatic tectonic plates some 15 million years ago, it is hard to understand how such relatively close relatives could have evolved independently on two such widely disjunct continents, one Gondwanic and the other Laurasian.

## PAEONIALES

Also centered in eastern Asia are the Paeoniales (Thorne, 1981) including two monogeneric families, Glaucidiaceae with only *Glaucidium palmatum* Sieb. & Zucc. of Japan and Paeoniaceae with 33 *Paeonia* L. species ranging from western Europe and northern Africa to eastern Asia and western North America. The two genera are linked not only by geographic distribution and usual mesic forest habitat but also by their rhizomatous perennial habit, unspecialized xylem, centrifugal initiation and maturation of stamens, apocarpy, low chromosome number ($n = 5$ or 10), and follicular fruit. Their closest relatives seem to be the somewhat more specialized Berberidales, also heavily represented in eastern Asia.

## BERBERIDALES

Asiatic relicts of the Berberidales include such monotypic or oligotypic families or subfamilies as the Sargentodoxaceae, Lardizabalaceae, Nandinaceae, Circeasteraceae, Lardizabalaceae, berberidaceous Ranzanoideae, and papaveraceous Pteridophylloideae. All of these taxa are restricted to eastern Asia except the Lardizabalaceae, which quite anomalously have two additional monospecific genera in central Chile (Thorne, 1972). Eastern Asia is well supplied too with most of the subfamilies and many of the genera of three larger families, Menispermaceae, Ranunculaceae, and Berberidaceae. One is tempted to consider eastern Asia the center of origin of this order. Two subfamilies of Papaveraceae, Eschscholzioideae and Platystemonoideae, however, are mostly or exclusively centered in western North America, and the monospecific Hydrastidaceae (Tobe and Keating, 1985), somewhat intermediate between the ranunculads and berberi-

dads, is indigenous only in eastern North America, being the sole endemic family in our Northeast. At the very least, this order can be considered as Laurasian in origin.

### NELUMBONALES—NYMPHAEANAE—RAFFLESIANAE

The related but widely distributed aquatic order Nelumbonales (Thorne, 1981, 1983) with the two monogeneric families Nelumbonaceae and Ceratophyllaceae are also indigenous in eastern Asia through Australasia. Likewise represented but more distantly related are the similarly aquatic and widely distributed nymphaeanean Cabombaceae and Nymphaeaceae, the latter with all three subfamilies present and one, the Hydrostemmatoideae (Barclayoideae), restricted to southeastern Asia. Another archaic group probably related to the Annonanae are the Rafflesianae, greatly reduced and specialized internal stem parasites, with three subfamilies present, Rafflesioideae of Indomalesia, Mitrastemonoideae of eastern Asia–Malesia and Central America, and the widely disjunct Apodanthoideae with a species of *Pilostyles* Guill. in Western Australia and another in the asiatic Near East. Unrepresented are the African–Mexican Cytinoideae and the African–South and Central American Hydnoraceae.

### HAMAMELIDALES

Among the numerous other relicts of eastern Asia are the Hamamelidales (Thorne, 1976) of the Rosanae (now including my former Hamamelidiflorae). Most archaic in the order are the Trochodendrineae with the primitively vesselless *Trochodendron aralioides* Seib. & Zucc. and *Tetracentron sinense* Oliv. of the Trochodendraceae and the genera *Cercidiphyllum* Sieb. & Zucc., *Euptelea* Sieb. & Zucc., and *Eucommia* Oliv., each representing a monogeneric family. All of these genera, once wide-ranging in the northern hemisphere, are now restricted to eastern Asia. Their common origin is indicated by their similar primitive xylem, leaf architecture, stomatal apparatus, pollen grains, and floral morphology. The fossil evidence for their once wide ranges furnishes a good warning to biologists that we must be aware that present distributions are not necessarily indicative of past distributions. Because some 23 genera (out of perhaps 31 genera) of the closely related Hamamelidineae are restricted to or represented in eastern

Asia, there is a strong possibility that the whole order also had its center of origin in eastern Asia and radiated out from there to other parts of the Laurasian supercontinent in Cretaceous or Paleogene time.

## SIMMONDSIACEAE

Closer to home in North America are several indigenous, and mostly endemic, taxa that until recently were misplaced or, in my earlier classifications, were *taxa incertae sedis*. In each case the dictum of geographic plausibility did supply or could have supplied the clue to their proper phylogenetic treatment. *Simmondsia chinensis* (Link) C. K. Schneid. (Thorne, 1985), an abundant evergreen dioecious shrub of the arid Southwest and a newly developed oilseed crop plant (jojoba or goatnut) producing a valuable, liquid wax, was long misplaced in the quite unrelated family Buxaceae. Morphologically *Simmondsia* seems most closely related to the Euphorbiaceae. Kakkar (1973) noted the similarity in leaf architecture of jojoba with that of species of *Euphorbia* L. with special reference to the bundle sheath and thick-walled cells at the vein endings.

However, the principal clue to the relationship was supplied by Scogin (1980), who found serological cross-reactivity between rabbit antiserum to *Simmondsia* seed protein and seed extracts from three species of the euphorbiaceous genera *Sapium* P. Br. of the Euphorbioideae and *Mallotus* Lour. and *Ricinus* L. of the Acalyphoideae. The seed extracts of other tested taxa showed no such cross-reaction. *Simmondsia* and *Sapium biloculare* (S. Wats.) Pax, whose seeds are among the famous Mexican jumping beans, often grow together in the Sonoran Desert. Because of its unique syndrome of chemical and morphological characteristics *Simmondsia* merits treatment as an independent family Simmondsiaceae in the Euphorbiales.

## CROSSOSOMATACEAE

Similarly misplaced for more than a century was the genus *Glossopetalon* A. Gray, attributed by its author with some misgivings to the Celastraceae. Re-examination of the genus morphologically and biochemically (Thorne and Scogin, 1978) showed that the genus, with several species indigenous in western North

America, should join *Crossosoma* Nutt. and the recently named genus *Apacheria* Mason in the Crossosomataceae, now a considerably expanded North American family.

The Crossosomataceae have at times been misplaced in the Dilleniinae due to the mistaken belief that the stamen initiation and maturation were centrifugal. It is found thriving commonly side by side with its similarly apocarpous or nearly apocarpous relatives of the Rosaceae, Crassulaceae, Saxifragaceae, and Hydrangeaceae. The insular species *Crossosoma californicum* Nutt., the theme plant of Southern California Botanists, is called Wild-apple by the residents of Santa Catalina Island, where it is often associated with its distant cousin, the rosaceous ironwood tree *Lyonothamnus floribundus* A. Gray.

## BATACEAE—GYROSTEMONACEAE—SAPINDACEAE

The Saltwort, *Batis maritima* L., a succulent-leaved sprawling dioecious shrub of our southern sea shores, was long misclassified near the equally halophytic chenopods and amaranths of the centrospermous Chenopodiales. Study of its disjunct monoecious cousin, *Batis argillicola* van Royen of northern Australia and Papua, gave us the clue to its probable relationship to the Australian Gyrostemonaceae and sapindaceous Dodonaeoideae, Stylobasioideae, and Emblingioideae (Thorne 1977; Carlquist, 1978c).

*Batis* resembles the Gyrostemonaceae, also fugitives from the Centrospermae, in their presumed anemophily; shrubby habit with relatively specialized stem anatomy; linear leaves with minute stipules; presence of glucosinolates or associated catalyzing enzyme; unisexual, apetalous flowers; isopolar, tricolporoidate, pertectate, non-baculate pollen grains; pistil with a single ovule in each locule; and septicidally-dehiscent fruits (in *Batis argillicola*).

The Gyrostemonaceae in turn have in common with the Dodonaeeae, in addition to their overlapping Australian ranges, shrubby habit; alternate, simple, entire, spatulate to commonly linear leaves with anomocytic stomata; apetalous, unisexual flowers with connate calyx 8-4-2-lobed or entire; stamens six to numerous on the top or rim of a convex or discoid receptacle; similar pollen grains; gynoecium of one or two to numerous, connate carpels with mostly free styles; ovary locules each with one axile, campylotropous, bitegmic ovule; fruit an indehiscent nutlet or

schizocarp in which each membranous carpel disperses separately from the others and the discoid axis; and curved seed with small, basal arillode. It is noteworthy that *Batis maritima* on our tropical American shores is closely associated with *Dodonaea viscosa* L. (Sapindaceae), *Scaevola plumieri* (L.) Vahl (Goodeniaceae), *Cassytha filiformis* L. (Lauraceae), and the abundantly naturalized *Casuarina equisetifolia* Forst. (Casuarinaceae), all with ultimately Australasian antecedents.

## ADDITIONAL NORTH AND SOUTH AMERICAN EXAMPLES

Many additional examples to show the efficacy of the principle of geographic plausibility could be discussed were space available. In North America one could list in addition the contiguity in the Southwest of the Fouquieriaceae (sometimes classified near the Old World Tamaricaceae) with the related Ericaceae and Ebenaceae; the anemophilous Garryaceae with the Cornaceae, Nyssaceae, and Alangiaceae (the last two families now extinct in the Southwest); and the Krameriaceae with the probably related Polygalaceae and the more completely tropical Trigoniaceae and Vochysiaceae.

Moving south to South America we could list for the Guayana Highlands the closely associated and related sarraceniaceous *Heliamphora* Benth. and Marcgraviaceae, Bonnetiaceae, Clusiaceae, and other thealean taxa; and commelinalean *Thurnia* Hook. f., Rapateaceae, Xyridaceae, and terrestrial Bromeliaceae. Farther south in Brazil there is heavy development of the closely related Mayacaceae and Commelinaceae and of the distantly related Velloziaceae and Pontederiaceae. The tropical American–African Canellaceae is commonly associated with many species of the related Annonaceae and Myristicaceae. In temperate South America one could cite as related and associated the Gomortegaceae, Lauraceae, and Monimiaceae; Malesherbiaceae, Caricaceae, Turneraceae, and Passifloraceae; Tropaeolaceae and geraniaceous Vivianioideae and Ledocarpoideae; and lilialean Philesiaceae and Alstromeriaceae.

Similar suites of related taxa could be listed for the other continents and the great island refugia of Madagascar and New Caledonia in addition to those taxa already discussed above. In developing my own classification plant geographic data have thus been most valuable in seeking out phylogenetic relationships, when used in conjunction with paleobotanical, host-parasitic, se-

rological, and comparative biochemical information as well as the usual morphological information gleaned from comparative studies of flowers, pollen grains, fruits, seeds, xylem and other stem anatomy, and leaf architecture. Two new approaches that show great promise in the study of angiosperm phylogeny are molecular taxonomic studies of chloroplast DNA and nuclear ribosomal DNA and cladistic methodology.

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# LATE CRETACEOUS AND TERTIARY FLORAS, VEGETATION, AND PALEOCLIMATES OF NEW ENGLAND

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## ABSTRACT

Late Cretaceous and Tertiary plant fossils are found in relatively few places in New England, but the fossil record is sufficient to provide a general impression of changes in floras, vegetation types, and climates in the region during this time span. Late Cretaceous pollen and plant megafossils of Massachusetts and Rhode Island are poorly known with regard to their affinities with modern taxa, but the fossils show that the subhumid paratropical Normapolles province of the eastern United States extended at least as far north as New England. Paleocene and early Eocene pollen assemblages from Massachusetts are important because they suggest that the tropical rainforests of the Gulf and Atlantic Coastal Plains extended with considerable taxonomic uniformity at least as far north as New England. The Eocene flora is quite similar to the coeval flora of Europe, partly because of migration from Europe to North America at the beginning of Eocene time. The late Oligocene pollen and megafossil flora of Vermont and the middle Miocene pollen flora of Massachusetts probably represent Mixed Mesophytic forest. One or both of these floras included exotic elements such as *Glyptostrobus, Podocarpus, Sciadopitys, Alangium,* Engelhardieae, *Phellodendron,* and *Turpinia.* Two pollen assemblages of probable Pliocene age are known from Martha's Vineyard; they represent a cool temperate vegetation.

Key Words: Cretaceous, Tertiary, palynology, paleobotany, New England

## INTRODUCTION

Late Cretaceous and Tertiary plant fossils occur in only a few places in New England (Figure 1, Table 1). The purpose of this paper is to evaluate the quality of fossil plant data available from New England and to combine plant megafossil and pollen data in order to arrive at a history of the Late Cretaceous and Tertiary floras, vegetation types, and climates in the region.

Late Cretaceous and Tertiary plant fossils in New England represent a total time span of about 93 to about 1.5 million years ago (Ma.), a total of slightly more than 90 million years (Figure 2). However, the fossil plant record is not a continuous one by any means; it is very spotty, and a much more fragmentary record than Figure 2 suggests. The problem is that beneath the glacial deposits that cover much of New England, most rocks in this region are older than Cretaceous.

Most Late Cretaceous and early Tertiary palynological studies

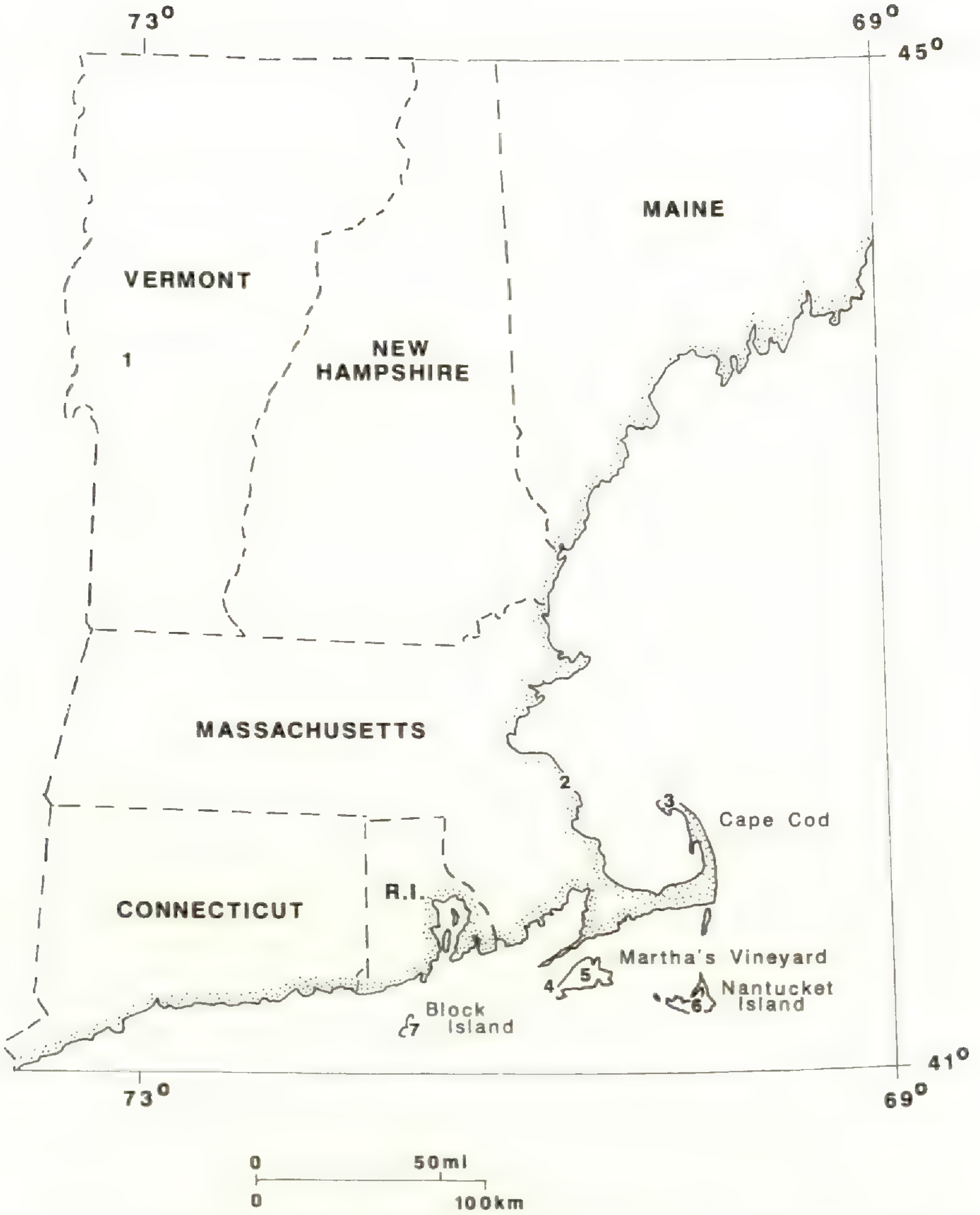


Figure 1. Map showing localities in New England from which Late Cretaceous and Tertiary plant fossils have been studied. Ages of deposits at each locality are given in Table 1.

in New England were concerned primarily with biostratigraphic problems. These studies generally disregarded spores and gymnosperm pollen, which typically have simple morphologies compared with angiosperm pollen; thus, spore and gymnosperm pollen species commonly have long stratigraphic ranges. Furthermore, Late Cretaceous megafloras in the region seem to include only

Table 1. List of Late Cretaceous and Tertiary plant localities in New England.

| Locality, Figure 1 | State | Locality Description | Age | Reference |
|---|---|---|---|---|
| 1 | VT | Village of Forestdale, northeast of Brandon | Probably late Oligocene | See references in Table 2 |
| 2 | MA | Scituate Third Cliff, Plymouth County | Miocene[1] | Frederiksen (1984a) |
| 2 | MA | North and south gravel pits, east of Marshfield Center, Plymouth County | Miocene[1] | Frederiksen (1984a) |
| 2 | MA | U.S. Geological Survey Marshfield Cranberry Bog no. 1 corehole, west of Marshfield, Plymouth County | Miocene[1] | Frederiksen (1984a) |
| 3 | MA | 3 wells near Holden's Pond, Cape Cod | Miocene?[1] | Zeigler et al. (1960), Groot and Groot (1964) |
| 4 | MA | Gay Head Cliffs, Martha's Vineyard | Miocene and Pliocene | Frederiksen (1984a) |
| 4 | MA | Gay Head Cliffs, Martha's Vineyard | Cenomanian to Campanian | Hollick (1906), Miller and Robison (1975), Tiffney (1977c) |
| 4 | MA | Zacks Cliffs, Martha's Vineyard | Miocene | Frederiksen (1984a) |
| 5 | MA | U.S. Geological Survey well ENW-50, east-central Martha's Vineyard | Cenomanian | Hall et al. (1980) |
| 6 | MA | U.S. Geological Survey borehole 6001, central Nantucket Island | Cenomanian; Coniacian to Campanian | Folger et al. (1978) |
| 7 | RI | Beach cliff outcrops in southeastern and northeastern Block Island | Turonian to Coniacian | Sirkin (1974) |

[1] Contains redeposited Late Cretaceous, Paleocene, and Eocene pollen.

sparse pteridophyte and gymnosperm fossils. Therefore, in this paper the emphasis is on angiosperm fossils, although gymnosperm pollen is abundant and important in the late Tertiary.

## LATE CRETACEOUS OF MASSACHUSETTS AND RHODE ISLAND

Hollick (1906), Miller and Robison (1975), and Tiffney (1977c) described the rich plant megafossil flora from Gay Head, Martha's Vineyard. The fossils consist mainly of leaves and include 4 species of ferns, 4 of gymnosperms, 2 of monocots, and about 80 of dicots. The specimens came from rocks assigned to the Raritan and Magothy Formations of New Jersey, which are Cenomanian to earliest Coniacian, and Coniacian to early Campanian in age, respectively (ages of Cretaceous formations are from Christopher, 1978, 1979; *see* Figure 2).

In addition to megafossils, Cretaceous pollen has also been found. In a borehole on Nantucket Island (Folger et al., 1978) the assemblages were Cenomanian, late Coniacian to Santonian, and Campanian in age; in a well on Martha's Vineyard (Hall et al., 1980), the pollen assemblage was Cenomanian; and in an outcrop on Block Island, Rhode Island (Sirkin, 1974), the assemblage was Turonian to Coniacian in age (Figure 2). Only a few stratigraphically important taxa were listed from each of these pollen assemblages, but apparently the entire assemblages are similar to those from New Jersey, which are fairly well known (Christopher, 1979, and references therein).

Hollick (1906) assigned many of his megafossils to modern genera, but it has since been found that these identifications with extant taxa are very unreliable even at the level of family or order (Wolfe and Upchurch, 1987). In addition, most Cretaceous plant megafossils cannot be linked to particular taxa of pollen and spores, which are also largely of uncertain affinity even at order level. Therefore, it is impossible to speak very meaningfully of the Late Cretaceous floras from North America in terms of modern taxa.

Some evidence exists as to the nature of the Late Cretaceous vegetation and climate on the East Coast, but the climatic evidence is equivocal. Parrish and Curtis (1982), Parrish et al. (1982), and Parrish (1987) presented a paleoclimatic model based on continental topography and positions of the continents. According

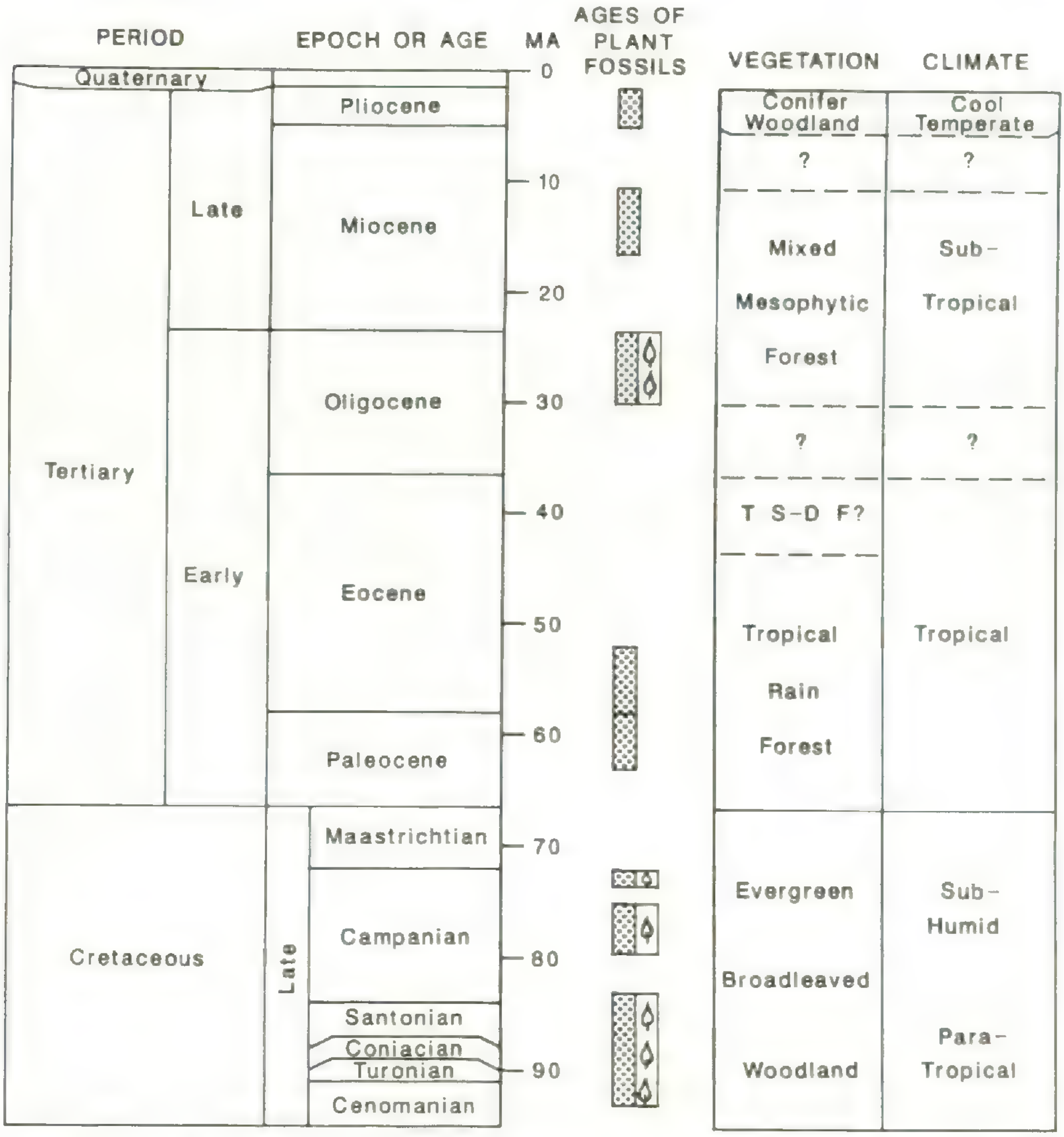


Figure 2. Ages of rocks in New England from which Late Cretaceous and Tertiary plant fossils have been studied (geochronologic ages from Berggren et al., 1985, and Hallam et al., 1985) and inferred vegetation types and climates of this time span in New England (Frederiksen, 1984a; Wolfe, 1985; Upchurch and Wolfe, 1987; Wolfe and Upchurch, 1987). Ma = megaannums = millions of years ago. Boxes only indicate maximum time spans that could be represented by known plant fossils. Dot pattern = pollen and spores; leaf pattern = megafossils. TS-DF = Tropical Semi-Deciduous Forest.

to this model, in the Late Cretaceous, the East Coast should have been humid all year because of the year-round presence of a subtropical high-pressure cell in the North Atlantic centered between 30° and 45°N lat. In contrast, studies of leaves, wood, and seeds (Wolfe and Upchurch, 1987; Upchurch and Wolfe, 1987) suggest that the Late Cretaceous of the East Coast was subhumid;

the vegetation apparently consisted of "open-canopy, broad-leaved evergreen woodland that existed under low to moderate amounts of rainfall evenly distributed through the year" (Wolfe and Upchurch, 1987, p. 33). At least both the Parrish and Wolfe-Upchurch models agree that rainfall was relatively constant throughout the year. Leaf characteristics also suggest that the climate was mainly paratropical, that is, the mean annual temperature was 20° to 25°C (Upchurch and Wolfe, 1987).

Judging by leaf characteristics, most taxa in the vegetation were evergreen rather than deciduous (Wolfe, 1987). A significant proportion of the flora was probably wind-pollinated: throughout the eastern United States, some of the most common pollen grains in Late Cretaceous strata belong to the Normapolles group and (in latest Cretaceous time) to the triporate group. The triporates were probably produced by Betulaceae, Juglandaceae, Myricaceae, and Ulmaceae (Thomson and Pflug, 1953; Crepet, 1981). The Normapolles group is much more heterogeneous morphologically and probably also in its botanical affinities (Zaklinskaya, 1981; Batten, 1984). However, some pollen of the Normapolles group was produced by wind-pollinated flowers of the Juglandales-Myricales complex (Friis, 1983) and, from morphological features of the dispersed pollen, it has long been thought that many taxa of the Normapolles group were wind-pollinated (*see* Frederiksen, 1985). The paradox thus arises that the presence of a distinct wind-pollinated element in the vegetation suggests a seasonally dry climate (Crepet, 1981; Batten, 1984), but leaf and wood characteristics indicate the lack of a pronounced dry season (Wolfe and Upchurch, 1987). Perhaps, as Crepet (1981) suggested, some degree of wind pollination was advantageous in the Cretaceous vegetation because not enough taxa of skilled pollinating insects had yet evolved. Alternatively, or concomitantly, the existence of open canopy vegetation and relatively low rainfall in the Late Cretaceous may have encouraged the development of wind pollination (Batten, 1984; Upchurch and Wolfe, 1987).

Phytogeographically, the Atlantic Coastal Plain was part of the Normapolles floristic province (Figure 3) that extended during Late Cretaceous and Paleocene time from the Midcontinental Seaway of North America to western Europe (Samoilovich, 1977; Zaklinskaya, 1977). For any particular time span in the Late Cretaceous, a considerable degree of similarity exists among pollen assemblages collected at sites from South Carolina to New

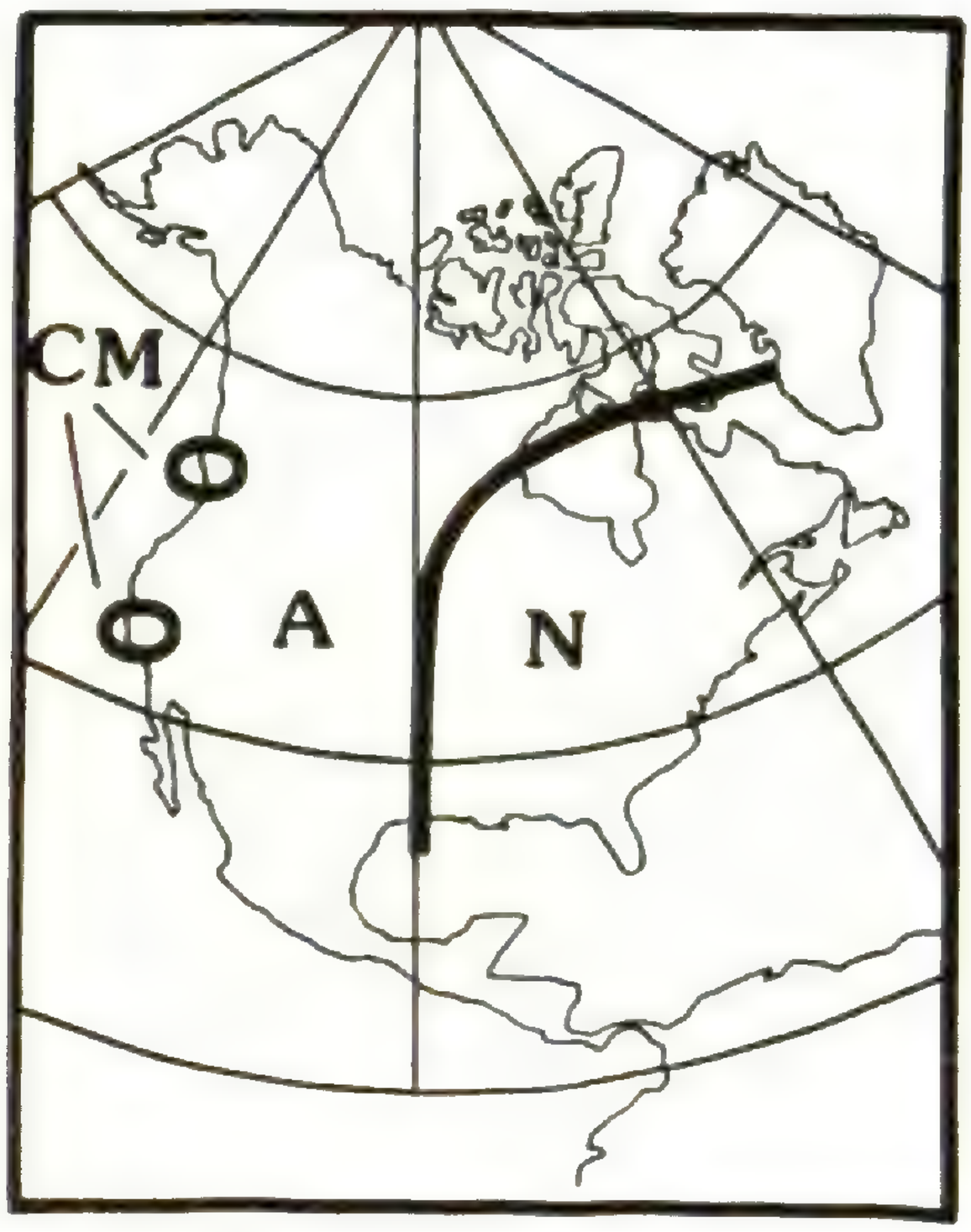


Figure 3. Map of latest Cretaceous floristic provinces in North America (from Frederiksen, 1987, Figure 1F; courtesy of *Palaios* and the Society of Economic Paleontologists and Mineralogists). A = *Aquilapollenites* province; CM = continental margin province; N = Normapolles province.

Jersey (Christopher, 1978). The pollen data from New England and sparse pollen data from offshore Canadian wells (Williams and Brideaux, 1975) indicate that the Late Cretaceous Normapolles province of North America extended, perhaps with little floristic change, at least as far north as southeastern Canada. The presence of rare *Aquilapollenites* pollen in Late Cretaceous assemblages from Massachusetts (Frederiksen, 1984a), New Jersey and Maryland (Evitt, 1973) may be a result of long-distance air transport of the pollen or may actually indicate a small but distinct floristic interchange with the *Aquilapollenites* province far to the west and north (Figure 3; Evitt, 1973).

## PALEOCENE OF MASSACHUSETTS

Very little is known about the Paleocene flora of New England because the plants are represented only by rare redeposited pollen of Paleocene age in Miocene strata of Plymouth County and in probable Miocene strata of Cape Cod, Massachusetts (Groot and Groot, 1964; Frederiksen, 1984a). "Redeposited" means that in

Miocene time, Paleocene rocks containing Paleocene pollen were exposed at the surface; these rocks were eroded by streams and waves, and the sediments, with their Paleocene pollen, were transported a short distance, and then deposited again to form a Miocene sediment. A fascinating aspect of the Miocene rocks is that they actually contain redeposited pollen of Late Cretaceous, Paleocene, and Eocene ages, all in the same samples, accompanied by indigenous Miocene pollen (Frederiksen, 1984a).

Redeposited Paleocene pollen from New England and sparse indigenous Paleocene pollen and spores in offshore Canadian wells (Williams, 1974; Williams and Brideaux, 1975) are similar to taxa known to the south in the Atlantic Coastal Plain and in the Gulf Coast. The pollen and spores suggest that the Normapolles province (modified floristically from its Cretaceous predecessor but still definable because of its Normapolles pollen) continued to extend at least as far north as southeastern Canada in the Paleocene.

Climatically, the Paleocene of the East Coast is thought to have been warmer and moister than the Late Cretaceous, leading to the widespread development of multistratal tropical rainforest (Upchurch and Wolfe, 1987). The most notable trends during the evolution of Paleocene pollen floras in eastern North America were (1) a low initial pollen diversity followed by a distinct increase in diversity, (2) rapid evolution of juglandaceous pollen forms, (3) first appearances of important pollen morphotypes such as *Carya, Symplocos,* thick-walled *Alangium,* Restionaceae, and *Proxapertites* (an extinct relative of the tropical brackish-water palm *Nypa*), and (4) a gradual reduction in number of species of the Normapolles group.

## EOCENE OF MASSACHUSETTS

Eocene floras of New England are known only from pollen redeposited into Miocene and possible Miocene strata in Massachusetts (Zeigler et al., 1960; Groot and Groot, 1964; Frederiksen, 1984a). From known ages of the pollen species elsewhere in eastern North America, it appears that this pollen in Massachusetts is entirely early Eocene in age. Therefore, no primary plant record exists for most of Eocene time in New England (Figure 2).

Based on morphologic features of fossil leaves from the Mis-

sissippi Embayment, western North America, and Greenland (that is, from localities far from New England), Wolfe (1985) suggested that the latest Paleocene to earliest Eocene vegetation of New England may have been tropical rainforest like the reconstructed vegetation of the same age in the Gulf Coast. Most Eocene pollen taxa had broad geographic ranges extending throughout the eastern United States, as shown by data in the many papers published on Eocene pollen from the upper Mississippi Embayment to the Gulf Coast, and north to Virginia (references in Frederiksen, 1979, 1980, 1988). The fairly rich Eocene pollen assemblage from Massachusetts and sparse Eocene pollen from Canadian offshore wells (Williams and Brideaux, 1975) indicate that the Eocene forests of the Gulf and Atlantic Coastal Plains extended with considerable or even large taxonomic uniformity as far north as southeastern Canada.

One of the most interesting features of the early Eocene flora of eastern North America is its considerable similarity to the coeval flora of western Europe. There is strong evidence for migration of both terrestrial vertebrates and plants across a northern land bridge between Europe and North America early in Eocene time (McKenna, 1975, 1983; Tiffney, 1985; Frederiksen, 1988). At least six plant taxa appear to have migrated from Europe to North America in early Eocene or possibly in very latest Paleocene time (Frederiksen, 1988), and these include the important genera *Platycarya* (Juglandaceae) and *Eucommia* (Eucommiaceae); this is the most distinct plant-migrational event known during early Tertiary time in North America. *Eucommia* was not found in the Eocene material in Massachusetts, but these assemblages did include four or five species or species groups within the *Platycarya* complex (*Platycarya* perplex of Wing and Hickey, 1984). Later in Eocene or early in Oligocene time, both *Eucommia* and *Platycarya* became extinct in North America and now are native only in eastern Asia.

## OLIGOCENE OF VERMONT

The fossil flora of Brandon, Vermont, has been extensively studied with regard to pollen, fruits and seeds, and wood (references in Table 2). A diverse flora has been identified, including at least 39 modern genera and generic groups (three of them tentatively identified) (Tables 2, 3). The age of this deposit has

Table 2. Modern genera in the Oligocene Brandon deposit that do not now occur in New England or whose geographic ranges are mainly south of New England. References for generic identifications: Spackman (1949), Traverse (1955), Eyde and Barghoorn (1963), Eyde et al. (1969), Tiffney and Barghoorn (1976, 1979), Tiffney (1977b, 1979, 1980, 1981, 1985). Taxa marked * were identified on the basis of megafossils but not pollen.

| Genus | Do Not Now Occur in U.S.; Mainly Found in Warmer Regions than Present New England | Occur in U.S. but Only South of New England | New England Is Near Northern End of Present Range |
|---|---|---|---|
| *Alangium* (Alangiaceae) | X | | |
| *Caldesia** (Alismataceae) | X | | |
| *Cleyera** (Theaceae) | X | | |
| *Cyrilla* (Cyrillaceae) | | X | |
| Engelhardieae (Juglandaceae) | X | | |
| *Euodia** (Rutaceae) | X | | |
| *Glyptostrobus* (Taxodiaceae) | X | | |
| *Gordonia* (Theaceae) | | X | |
| *Ilex* (Aquifoliaceae) | | | X |
| *Illicium** (Illiciaceae) | | X | |
| *Liquidambar* (Hamamelidaceae) | | | X |
| *Ludwigia* (Onagraceae) | | | X |
| *Magnolia** (Magnoliaceae) | | | X |
| *Manilkara-Mimusops* group (Sapotaceae) | | X | |
| *Microdiptera** (Lythraceae) | X | | |

Table 2. Continued.

| Genus | Do Not Now Occur in U.S.; Mainly Found in Warmer Regions than Present New England | Occur in U.S. but Only South of New England | New England Is Near Northern End of Present Range |
|---|---|---|---|
| *Nyssa* (Nyssaceae) | | | X |
| *Persea** (Lauraceae) | | X | |
| *Phellodendron** (Rutaceae) | X | | |
| *Planera* (Ulmaceae) | | X | |
| *Pterocarya* (Juglandaceae) | X | | |
| *Symplocos* (Symplocaceae) | | X | |
| *Turpinia** (*Staphyleaceae*) | X | | |
| *Vitis* (Vitaceae) | | | X |
| *Zanthoxylum** (Rutaceae) | | | X |

Table 3. Modern taxa recorded from the Oligocene pollen flora of Vermont (Traverse, 1955) and the Miocene pollen flora of Massachusetts (Frederiksen, 1984a).

| | Miocene | Oligocene |
|---|---|---|
| TREES | | |
| **Gymnosperms** | | |
| Pinaceae | | |
| *Abies* | ? | |
| *Larix* | ? | |
| *Picea* | X | |
| *Pinus* | X | X |
| *Tsuga* | X | |
| Podocarpaceae | | |
| *Podocarpus* | X | |
| Taxodiaceae-Cupressaceae-Taxaceae | X | |
| *Glyptostrobus* | | X |
| *Sciadopitys* | X | |
| **Dicotyledons** | | |
| Alangiaceae | | |
| *Alangium* | | X |
| Aquifoliaceae | | |
| *Ilex* | X | X |
| Betulaceae | | |
| *Alnus* | X | |
| *Betula* | X | |
| *Corylus* | X | ? |
| Clethraceae | | |
| *Clethra* | | ? |
| Cornaceae | ? | |
| Cyrillaceae | | |
| *Cyrilla-Cliftonia* | X | X |
| Fagaceae | | |
| *Castanea* | X | X |
| *Fagus* | X | X |
| *Quercus* | X | X |
| Hamamelidaceae | | |
| *Liquidambar* | X | X |
| Juglandaceae | | |
| *Carya* | X | X |
| Engelhardieae | X | X |
| *Juglans* | X | X |
| *Pterocarya* | X | X |
| Moraceae | | |
| *Morus* | ? | X |
| Nyssaceae | | |
| *Nyssa* | X | X |
| Platanaceae | | |
| *Platanus* | X | |

Table 3. Continued.

| | Miocene | Oligocene |
|---|---|---|
| Rhamnaceae | | |
| *Rhamnus* | | X |
| Rosaceae | | ? |
| Rutaceae | | |
| Toddalieae | | X |
| Salicaceae | | |
| *Salix* | X | |
| Sapotaceae | X | X |
| Symplocaceae | | |
| *Symplocos* | X | X |
| Theaceae | | |
| *Gordonia* | X | X |
| Tiliaceae | | |
| *Tilia* | X | X |
| Ulmaceae | | |
| *Planera* | | X |
| *Ulmus-Zelkova* | X | X |
| LOW SHRUBS, HERBS, VINES | | |
| Anacardiaceae | | |
| *Rhus* | | X |
| Chenopodiaceae-Amaranthaceae | X | |
| Compositae, short-spined | | |
| and long-spined | X | |
| Cyperaceae | ? | |
| Elaeagnaceae | ? | |
| Ephedraceae | | |
| *Ephedra* | ? | |
| Ericaceae | X | X |
| Gramineae | X | X |
| Malvaceae | X | |
| Myricaceae | | |
| *Comptonia* | ? | |
| *Myrica* | X | |
| Onagraceae | | |
| *Ludwigia* | X | X |
| Santalaceae | | |
| *Nestronia* | | ? |
| Umbelliferae | X | |
| Vitaceae | | |
| *Parthenocissus* | | X |
| *Vitis* | | X |
| AQUATICS AND SEMIAQUATICS | | |
| Haloragidaceae | | |
| *Myriophyllum* | X | |
| Sparganiaceae-Typhaceae | | |
| *Sparganium-Typha* | X | |

not been precisely determined, but it represents a small slice probably of late Oligocene or possibly of earliest Miocene time (B. H. Tiffney, written comm., 1981); in this paper it will be considered late Oligocene in age.

Some of the most striking aspects of the Brandon swamp flora and vegetation are the scarcity of herbs and gymnosperms and the abundance of dicotyledonous trees and shrubs (Traverse, 1955; Tiffney, 1977a). Pollen thought to have been produced by herbs is generally not abundant in early Tertiary rocks of eastern North America, and some of the herb pollen genera identified in Paleocene and Eocene rocks seem to have become extinct in this region by the end of the Oligocene (e.g., *Pistillipollenites,* Gentianaceae; *Milfordia,* Restionaceae). Furthermore, during most of early Tertiary time, many herb niches were occupied by pteridophytes and not by angiosperms (Frederiksen, 1985). Many families of herbs had evolved in the Northern Hemisphere by the end of Oligocene time (Daghlian, 1981; Muller, 1981), but pollen of these families is rare in Oligocene rocks and is commonly sparse even in Miocene rocks of eastern North America (Traverse, 1955; Leopold, 1969; Rachele, 1976; Frederiksen, 1980, 1984a, 1984b, 1988; Owens et al., in press). In short, late Oligocene samples from eastern North America generally lack the typical Paleocene and Eocene herb pollen taxa, and they also lack the herb pollen types that are probably restricted to the late Tertiary and Quaternary in this region (Table 3).

## COMPARISON OF EOCENE AND OLIGOCENE FLORAS

The distinction between the Eocene pollen flora of Massachusetts and the Oligocene pollen flora of Vermont may not be immediately obvious because only a moderate number of Eocene genera have actually been found in Massachusetts (Frederiksen, 1984a). However, if much larger lists of early to middle Eocene pollen taxa from Virginia and South Carolina are examined (Frederiksen, 1979, 1980, 1984b), a considerable difference can be seen between the Eocene flora of the Atlantic Coastal Plain and the Oligocene flora of Vermont, particularly with regard to zoophilous forms. Many wind-pollinated taxa listed by Traverse (1955; *see* Table 3 of this paper) from the Brandon deposit were also found in the Eocene, for example, Pinaceae and Taxodiaceae-Cupressaceae-Taxaceae; Engelhardieae, *Pterocarya, Juglans,* and *Carya*

of the Juglandaceae; *Castanea* and *Quercus* types of the Fagaceae; *Ulmus* and *Planera* types of the Ulmaceae. Some taxa having zoophilous pollen are also represented in floras of the two time spans, for example, Alangiaceae (*Alangium*), Anacardiaceae (*Rhus*), Aquifoliaceae (*Ilex*), Cyrillaceae, Nyssaceae, Sapotaceae, Symplocaceae, and Tiliaceae (*Tilia* type). However, the early and middle Eocene pollen floras of the Atlantic Coastal Plain contain many angiosperm taxa that became extinct before the end of the Eocene; these extinct taxa are probably mainly zoophilous, and they give the Eocene floras a much warmer climatic appearance than the Oligocene flora from Brandon.

The known Eocene and Oligocene floras of New England were different partly because they were separated by at least 20 m.yr. in age (52–58 Ma. vs. perhaps 24–30 Ma.). Evolution, extinction, and climatic change had been active during this time span. As noted above, the Eocene flora of Massachusetts is early Eocene in age; the early Eocene was the warmest part of the entire Tertiary in North America (Wolfe and Poore, 1982; Wolfe and Upchurch, 1987). In contrast, the Brandon flora postdates the Oligocene climatic deterioration (of Wolfe, 1971 = the terminal Eocene event of Wolfe, 1978); this rapid cooling (and drying?) event probably commenced at the beginning of Oligocene time, at least on the Gulf Coast (Frederiksen, 1988). Thus, between early Eocene and late Oligocene time, the vegetation of New England had probably changed from tropical rainforest to deciduous broadleaved forest (Wolfe, 1985) or Mixed Mesophytic forest (Figure 2).

## MIOCENE OF MASSACHUSETTS

The Miocene pollen flora of Massachusetts is quite well known because it has been found at six localities in Plymouth County and Martha's Vineyard (Frederiksen, 1984a). One of these outcrops has been dated as middle Miocene in age on the basis of vertebrate fossils. The exact ages of the remaining five localities have not been independently established, but they all have similar pollen assemblages. Because they all seem to represent vegetation of the mid-Miocene warming, which was restricted to the late early and early middle Miocene (Wolfe, 1985), they are probably all similar in age. The Miocene flora is rich in taxa of both gymnosperm and dicotyledonous trees and is relatively rich in taxa of low shrubs, herbs, and vines (Table 3).

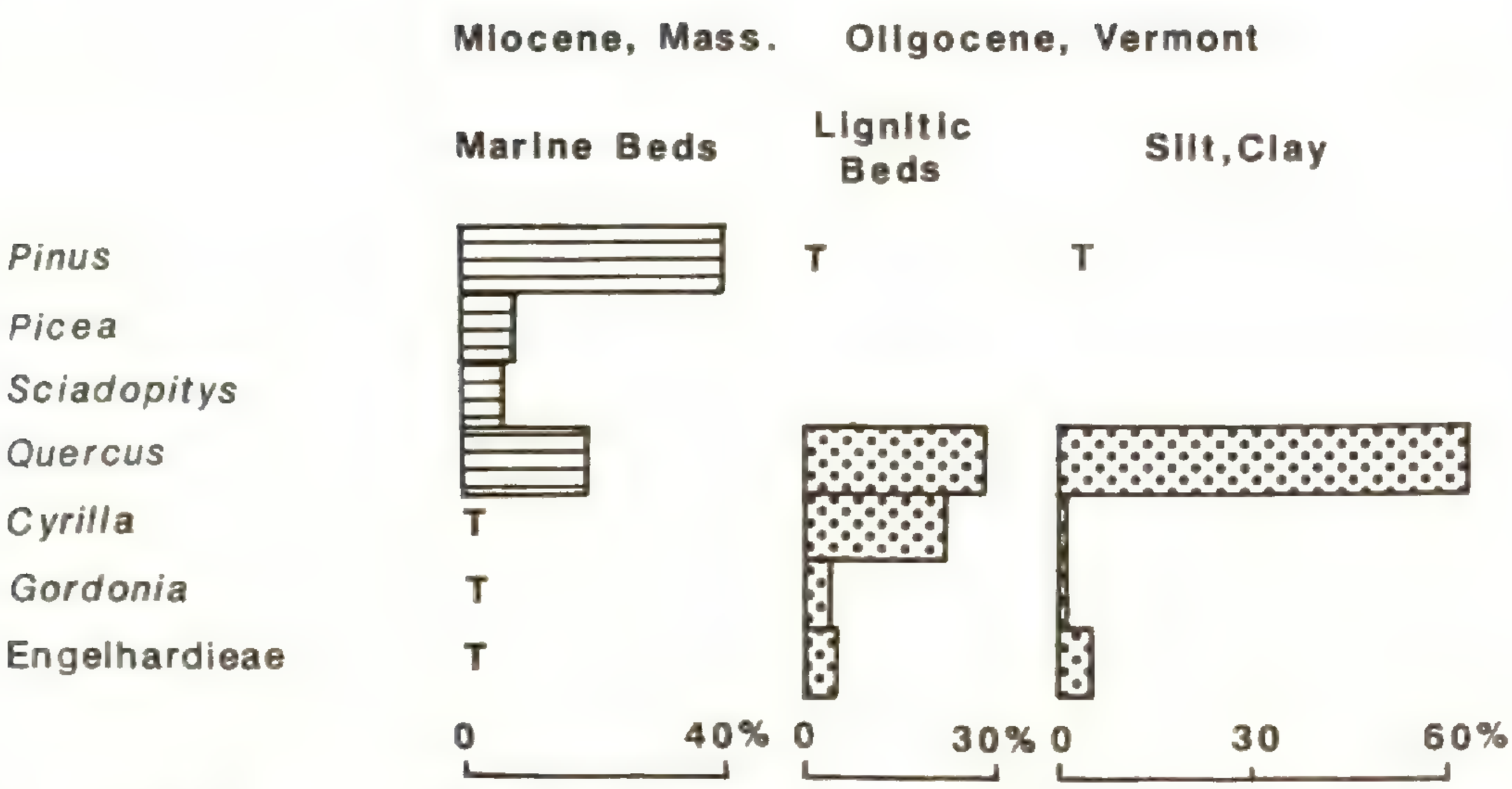


Figure 4. Relative frequencies of the more abundant pollen types in the Oligocene of Vermont (Traverse, 1955) and the Miocene of Massachusetts (Frederiksen, 1984a). T = trace = <1%.

## COMPARISON OF OLIGOCENE AND MIOCENE FLORAS

Table 3 compares the Oligocene and Miocene pollen floras of New England. Both floras have about the same taxa of dicotyledonous trees. The apparent absence of *Alnus, Platanus,* and *Salix* from the Oligocene flora is surely due to ecological factors. *Alangium* is present in the Oligocene flora of Vermont but was not observed in the Miocene flora of Massachusetts; however, pollen of this genus has been found in middle Miocene samples from New Jersey (Wolfe and Tanai, 1980; Owens et al., in press). The presence of *Betula* in the Miocene but not in the Oligocene suggests a slightly cooler climate in Miocene time; similarly, *Planera,* a genus presently restricted to the Southeast in the United States, which was found in the Oligocene but not the Miocene, suggests a slightly warmer climate in Oligocene time.

The most obvious difference between the Oligocene and Miocene floras is in the higher diversity of conifers and low shrubs, herbs, and vines in the Miocene than in the Oligocene flora. On the Atlantic Coastal Plain, *Sciadopitys* is probably restricted to the Miocene (Frederiksen, 1984a). The paleoclimatic significance of this genus in the Tertiary is difficult to evaluate except that it was much more widely distributed in the Northern Hemisphere in Tertiary time than now and therefore must have had a broader climatic range (Frederiksen, 1985). The apparent lack of *Podo-*

*carpus* pollen in the Oligocene flora is surprising, as pollen of this genus is common in Cretaceous and lower Tertiary rocks of the eastern United States, and it is found in most Miocene samples from Massachusetts (Frederiksen, 1984a). *Pinus* pollen is sparsely represented in the Oligocene samples, even in assemblages from clay and silt that contain largely pollen from outside the peat swamp, whereas pine pollen is 36–45% of the entire pollen assemblage in Miocene samples from Massachusetts (Frederiksen, 1984a) (Figure 4). Pine trees produce enormous amounts of pollen; thus, pines must have lived at some distance from the Brandon depositional basin.

As regards low shrubs, herbs, and vines of the two floras, the most significant difference is the presence of Compositae and Umbelliferae pollen in the Miocene flora and the absence of pollen of these families in the Oligocene assemblage. Compositae pollen is rare if present at all in Oligocene deposits, and for most practical purposes it first appears at the beginning of the Miocene (Muller, 1981). Umbelliferae pollen has been found in Europe in rocks as old as Eocene (Muller, 1981), but it has not been recognized in North America in lower Tertiary strata. Thus, the apparent absence of Compositae and Umbelliferae fossils from the Brandon flora probably has age or possibly paleoecologic rather than paleoclimatic significance. Surely Chenopodiaceae-Amaranthaceae, *Myrica, Myriophyllum,* and *Sparganium-Typha* are lacking from the Brandon Oligocene pollen assemblages only for paleoecologic reasons. The marsh herb *Caldesia* (Alismataceae) has been identified in the Oligocene flora on the basis of fruits (Tiffney, 1985).

Differences exist between the Oligocene and Miocene floras of New England with regard to exotic elements, that is, modern genera that no longer live in the United States, but the differences are difficult to evaluate. Ten such genera or generic groups were found in the Brandon deposit (Table 2), but six of them (*Caldesia, Cleyera, Euodia, Microdiptera, Phellodendron, Turpinia*) were found only as megafossils, not as pollen, no doubt because they are zoophilous. In addition, the Brandon seed and fruit flora includes the extinct genera *Moroidea* (Moraceae) and *Caricoidea* (Cyperaceae) as well as Myrtaceae? (B. H. Tiffney, written comm., 1988). The exotic genera and generic groups *Alangium, Glyptostrobus,* Engelhardieae, and *Pterocarya* were found as pollen in the Brandon deposit; most or all of these probably existed in New England in Miocene time as well. In addition, the Miocene pollen

assemblages include *Sciadopitys* and *Podocarpus*. In short, as far as can be determined from pollen, the Miocene flora of New England included at least as many exotic modern genera as the Oligocene flora.

It is not easy to compare the vegetation and climate of the Vermont Oligocene with the vegetation and climate of the Massachusetts Miocene, particularly because both sets of deposits lack fossil leaves that are critical for quantitative climatic analysis. In fact, only small Oligocene or late Tertiary leaf floras are available from anywhere in eastern North America (Wolfe, 1978). In the following paragraphs, I summarize conclusions about the Oligocene of Vermont, then about the Miocene of Massachusetts, and then compare the two.

The flora of the Brandon deposit shows that the late Oligocene climatic regime in the area was distinctly warmer than now (Table 2). Traverse (1955) considered the Oligocene flora of Vermont to be most similar to the extant flora of the southeastern United States. Tiffney (1977a) and Wolfe (1979) noted that the Brandon flora appeared to contain both evergreen and deciduous broadleaved elements; Tiffney regarded the climatic affinity as being subtropical to paratropical. Wolfe (1979, p. 26) stated that the Brandon flora may represent evergreen broadleaved forest, but later (1985) he considered the Brandon flora to represent deciduous broadleaved forest that lay to the north of evergreen broadleaved forest.

Considering the taxa present in the Miocene pollen flora (Table 3) and relative frequencies of the various pollen types (Figure 4), Frederiksen (1984a) concluded that the Miocene flora of Massachusetts represented high-diversity low-dominance Mixed Mesophytic forest somewhat similar to the modern forest of the central to southern Appalachian Mountains except that the Miocene forest had a larger component of conifers than the modern Appalachian forest. On the basis of sparse plant megafossils, Wolfe (1977, p. 48) also thought that the Miocene vegetation of the eastern United States was probably Mixed Mesophytic forest.

The main question regarding the late Oligocene and middle Miocene vegetation of New England is the role of conifers in the lowland forests of the two time spans. In his 1985 vegetation map, Wolfe (1985, Figure 11) combined data from the late Oligocene and early Miocene and showed New England as dominated by deciduous broadleaved forest with the northern Appalachian Mountains covered by mixed coniferous forest. In this view, ap-

parently, most conifers were in the uplands, and this would explain why conifer pollen and megafossils are so scarce in the Oligocene Brandon lowland deposit in which the plant fossils (at least in the lignite) represent the local flora. In contrast, conifer pollen is abundant in assemblages from Miocene marine strata of Massachusetts, which represent the regional flora (Figure 4). Does this Miocene pollen reflect abundance of conifer trees in the lowland vegetation of the time (the interpretation of Frederiksen, 1984a), or did the conifer pollen come mainly from the uplands (apparently the interpretation of Wolfe, 1985)? Probably both interpretations are correct to some extent. For example, *Picea* and *Tsuga* are unlikely to have grown in close proximity to *Cyrilla-Cliftonia, Gordonia,* Sapotaceae, and *Symplocos* in the lowland Miocene forests. On the other hand, *Pinus, Sciadopitys,* and possibly *Podocarpus* may have lived in the warm lowlands. It seems unlikely that a 40% relative abundance of pine pollen in the Miocene marine sediments could be due entirely to long-distance transport from the mountains. Additionally, *Sciadopitys* trees were very abundant in some Miocene lowland peat swamps of northwestern Europe (Thiergart, 1949).

In summary, differences between the Oligocene and Miocene pollen floras are obvious but somewhat difficult to interpret especially with respect to vegetation types and paleoclimates. Differences in dicotyledonous tree taxa of the two time spans are minimal (Table 3). The presence in the Miocene pollen assemblages of *Abies*(?), *Larix*(?), *Picea, Tsuga,* and *Betula* and the much higher relative frequencies of conifer pollen in the Miocene assemblages are undoubtedly partly an effect of regional as opposed to local pollen catchment, but conifers appear to have been more abundant (and the climate perhaps a little cooler) in New England in middle Miocene than in late Oligocene time. However, the lowland vegetation of both time spans could probably be termed Mixed Mesophytic forest. Other differences between the Oligocene and Miocene floras are results of evolution (Compositae and Umbelliferae in Miocene assemblages) and immigration followed by regional extinction (*Sciadopitys* in Miocene assemblages).

## PLIOCENE OF MASSACHUSETTS

Two pollen samples of Pliocene (or possibly latest Miocene) age are known from Martha's Vineyard (Frederiksen, 1984a). These samples contain very low-diversity assemblages that con-

Table 4. Taxa recorded from Pliocene pollen and spore assemblages of Massachusetts (Frederiksen, 1984a).

| |
|---|
| TREES |
| **Gymnosperms** |
| *Picea* |
| *Pinus* |
| **Dicotyledons** |
| *Alnus* |
| *Betula* |
| LOW SHRUBS, HERBS, VINES |
| Caryophyllaceae? |
| Compositae, short-spined |
| Ericaceae |
| Gramineae |
| *Myrica*? |
| PTERIDOPHYTES AND BRYOPHYTES |
| *Botrychium*? |
| *Lycopodium* |
| *Selaginella* |
| *Sphagnum* |

sist mostly of pollen of *Pinus,* shrubs and herbs, and spores of *Sphagnum* and pteridophytes (Table 4). The climate in which the flora lived was probably cool temperate. This flora is far less diverse than that of the Miocene, and no exotics have been found among the Pliocene spore and pollen taxa.

## CONCLUSIONS

The Late Cretaceous and Tertiary plant fossil record of New England consists of megafossils from the Late Cretaceous and Oligocene epochs and pollen from the Late Cretaceous and from each epoch of the Tertiary (Figure 2). The fossils represent only bits and pieces of the time span between 93 and 1.5 Ma. However, the data points in New England, and data from elsewhere in North America, are sufficient to demonstrate distinct changes in floras and vegetation types corresponding to a change of climate that was paratropical in the Cretaceous, reached a maximum warmth in the early Eocene, and then cooled into the Pliocene and of course became even colder in the Quaternary.

This paper shows that, to obtain a Late Cretaceous and Tertiary floral, vegetational, and climatic history of New England, mega-

fossil evidence is critical for reconstructing vegetation and climate, but only a few time spans are represented by megafossils in this region; most of the plant megafossil data come from rather far away. On the other hand, the pollen assemblages contribute much of the total floral data, because they represent many more geologic time data points in New England itself than do the megafossils.

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# PLEISTOCENE AND HOLOCENE FLORAS OF NEW ENGLAND AS A FRAMEWORK FOR INTERPRETING ASPECTS OF PLANT RARITY

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## ABSTRACT

The times of arrival from southern sources and the rates and directions of migration are now known for many species of forest trees in New England. This information has made possible the reconstruction of generalized vegetation types for the period 14,000 to 9000 yr. B.P., as has been done recently by R. Davis and G. Jacobson for Vermont, New Hampshire, and Maine. The regional pattern, which has been based mainly on studies of fossil pollen from wind-pollinated trees, includes a diverse and biogeographically interesting flora of bryophytes, herbs, and shrubs that only recently is becoming defined through studies of plant macrofossils. The most thoroughly investigated sites, Tom Swamp (Massachusetts), Columbia Bridge (Vermont), and Upper South Branch Pond (Maine) have produced late-glacial floras with numerous calcicoles, some of which are rare or lacking in the present New England flora. Fossils of arctic-alpine species are also present at these sites, which are all at low elevations. A prominent calcicole element exists in the late-glacial fossil record regardless of whether the extant flora near a site contains such plants. This pattern is evident for both seed plants and bryophytes. For areas with acidic soils, the loss of calcicoles is correlated with the late-Pleistocene arrival of spruce (as documented by increases in macrofossils) at 12,800 yr. B.P. in southern New England, and some 2300 radiocarbon years later in north-central Maine. Leaching, humus or litter accumulation, and other aspects of soil genesis may have been responsible for the loss, but what caused the pattern is poorly understood. As viewed on a continental scale and over thousands of years, the elimination of calcicoles has left fragmented ranges and rare occurrences in eastern North America of boreal or northern plants that otherwise are today widespread to the west.

Key Words: Arctic-alpine plants, biogeography, calcicoles, late-Pleistocene floras, New England, paleoecology, plant macrofossils, plant rarity

## INTRODUCTION

The New England flora assembled from diverse sources during and after late-Pleistocene deglaciation. The margin of the continental ice sheet had reached a terminal position south of Cape Cod 18,000 radiocarbon years Before Present (yr. B.P.), and by ca. 12,000 yr. B.P. the margin was located in the St. Lawrence River Valley (Dyke and Prest, 1987). Studies of fossil pollen throughout this region (M. Davis, 1983; R. Davis and Jacobson, 1985), show that successive immigrations of populations of various tree species took place during the late Pleistocene and Ho-

locene after an initial period in which trees were sparse or absent and plant communities consisted of mosses, herbs, and shrubs. An analysis of 47 radiocarbon-dated pollen or plant macrofossil records from northern New England and adjacent Canada showed tundra, woodland, and forest vegetational phases extending one after another across northern New England between 14,000 and 9000 yr. B.P. (R. Davis and Jacobson, 1985). Poplar, spruce, paper birch, jack pine, balsam fir, tamarack, ironwood-ash-elm, oak, maple, white pine, and hemlock arrived in that order and spread in time-transgressive migrations generally northward across this region, with, however, some local differences in sequence and timing due to elevation and other factors.

Much of the late-Quaternary paleobotanical record of New England consists of changing percentages and accumulation rates of pollen from various wind-pollinated forest trees, which are only a small subset of the total flora. Alternative or supplementary sources of information about the history of this flora, although little explored at present, are from seeds, fruits, leaves, and other vegetative structures (plant macrofossils; Birks, 1980) occurring dispersed in lake, peatland, and alluvial sediments (Anderson et al., 1986; Pierce and Tiffney, 1986). Because plant macrofossils are less apt than pollen to be transported over long distances, they are a sample of the vegetation that once existed near the site of recovery. This circumstance, coupled with the greater potential of identification to species than can be achieved for many common pollen types, makes macrofossils highly useful biogeographically.

In this paper I summarize my and other recent studies of late Quaternary plant macrofossils from sites in New England. I use these data to explore connections between late Pleistocene and contemporary floras and to provide a temporal setting for the development of three related patterns of plant rarity, namely arctic-alpine species, northern calcicoles, and the "western" North American element in the flora of New England and nearby areas. My approach is floristic and involves the relationship between where certain species now occur in New England and where they were in the past in this region, as well as the factors or events that can be correlated with changes in distribution. Studies of both vascular plant and bryophyte fossils are included, the latter primarily as a source of information about the edaphic character of late-glacial terrestrial environments.

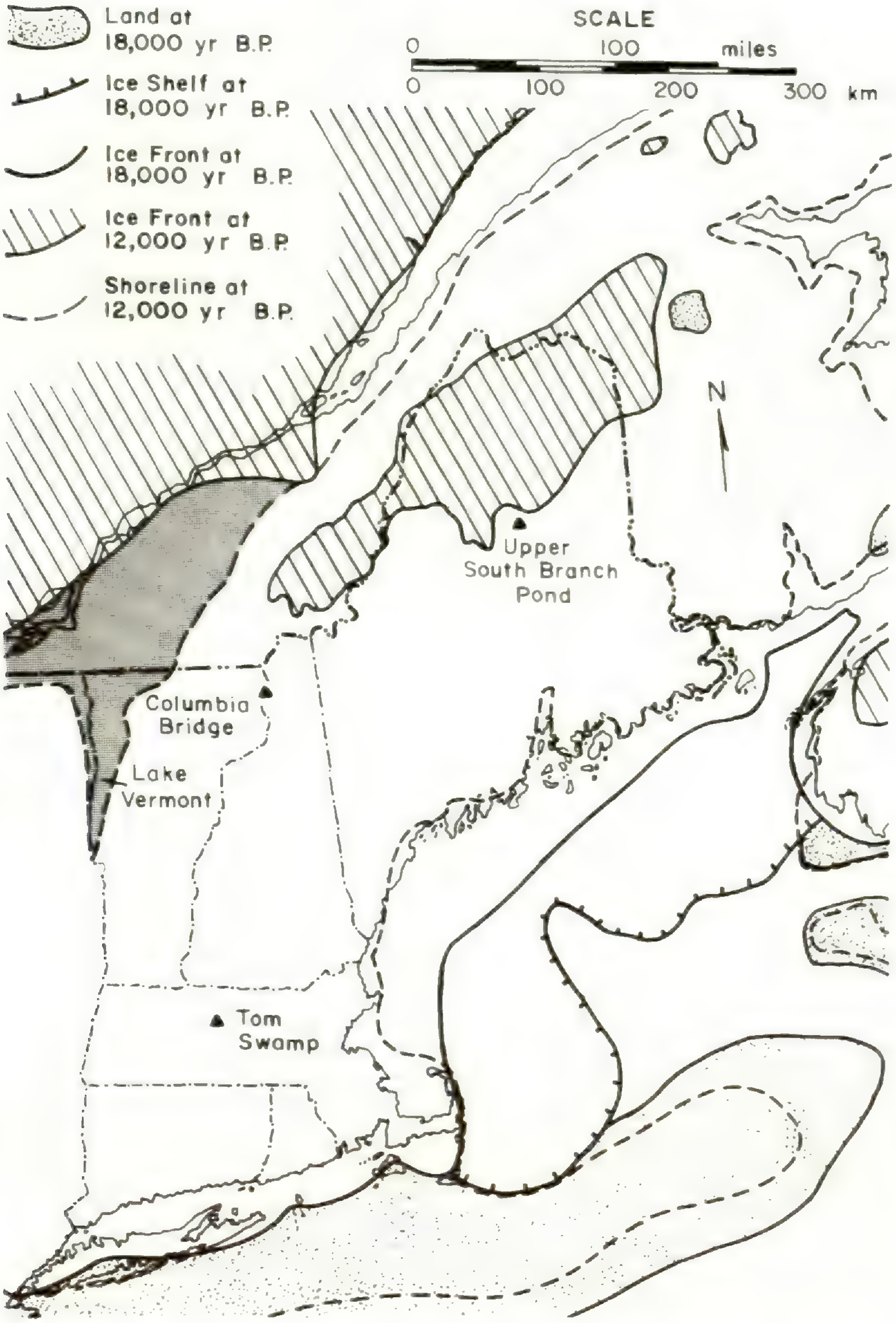



Figure 1. Map of New England and adjacent areas showing position of ice margins and other landscape features at 18,000 and 12,000 yr. B.P. (after Dyke and Prest, 1987). Triangles indicate location of sites discussed in the text.

## SITE DESCRIPTIONS AND METHODOLOGY

Studies at Tom Swamp (Massachusetts), Columbia Bridge (Vermont), and Upper South Branch Pond (Maine) have produced large and diverse late-Pleistocene plant macrofossil assemblages. Other studies of macrofossils in New England (Argus and Davis, 1962; Tolonen and Tolonen, 1984) provide supporting data. The small number of sites from which published records are available does not imply that plant macrofossils are uncommon in New England Pleistocene and Holocene deposits, but indicates instead that most Quaternary paleoecological studies in the region have focused on pollen.

The fossil floras described here are from distant parts of New England (Figure 1), and their depositional settings also differ in a number of ways (Table 1). The Columbia Bridge flora (Miller and Thompson, 1979) was the first late-glacial macrofossil assemblage in New England to be studied in detail using modern techniques. Because it included numerous calcicoles, reflecting perhaps the local presence of calcareous bedrock and glacial drift, study sites for comparison were sought in areas of acidic bedrock. Those selected were Upper South Branch Pond (Anderson et al., 1986) and Tom Swamp (M. Davis, 1958; Gaudreau, 1986) on which related paleoecological studies had been undertaken by other investigators. The three sites have been thoroughly radiocarbon dated, and stratigraphic pollen data are available for all of them.

Plant macrofossil stratigraphies have been published for Upper South Branch Pond (late Pleistocene and Holocene vascular plants and mosses; Anderson et al., 1986) and Tom Swamp (late Pleistocene bryophytes; Miller, 1987a). Presented here are stratigraphic data for vascular plant macrofossils recovered from the late Pleistocene and early Holocene sediments at Tom Swamp. In contrast to the other two records, the Columbia Bridge plant macrofossils (Miller and Thompson, 1979; Miller, 1987b) appear to have been deposited during a short period of time. Because their distribution did not change in any obvious pattern within the sampled stratigraphic interval, the fossils are treated as a single assemblage.

The macrofossils came from sediments collected either with a piston corer operated from the peatland or lake surface (Tom Swamp, Upper South Branch Pond) or by digging by hand at an

Table 1. Site characteristics of late-Quaternary plant macrofossil floras in New England.

| Character | Tom Swamp[1] | Columbia Bridge[2] | Upper South Branch Pond[3] |
|---|---|---|---|
| Location | 42°31′N, 72°13′W; Worcester Co., MA | 44°51′N, 71°33′W; Essex Co., VT | 46°5′N, 68°54′W; Piscataquis Co., ME |
| Elevation | 232 m | 301 m | 300 m |
| Present setting | 250-ha peatland | outcrop of laminated sand, silt, and clay of proglacial (?) lake of unknown size | 34-ha lake |
| Bedrock geology | aluminous mica and quartzose schists, aluminous phyllite | quartz-muscovite phyllite and schist, calcareous mica schist, quartzose and micaceous crystalline limestone | rhyolite |
| Age | 12,830 ± 120 yr. B.P.<br>11,580 ± 110 yr. B.P.<br>10,080 ± 100 yr. B.P. | 11,390 ± 115 yr. B.P.<br>11,540 ± 110 yr. B.P. | 11 dates, 10,965 ± 230 to 230 ± 70 yr. B.P. |

[1] Miller, 1987a; this paper.
[2] Miller and Thompson, 1979.
[3] Anderson et al., 1986.

outcrop (Columbia Bridge). The fossils were concentrated by flushing fine-grained sediment particles through a 250 or 500 $\mu$m sieve after the samples had been disaggregated in tap water, warm 10% KOH, or warm 5% $Na_2CO_3$. Plant fossils removed from the residues under low-power magnification were identified by comparing them with a reference collection derived from critically determined herbarium specimens. It was sometimes necessary to use special techniques (scanning electron microscopy, anatomical sections, removing the outer layers of seeds and fruits) to attain acceptable comparisons. The geographic scope of the reference collection proved to be an important consideration because the fossils sometimes represented species unknown in the present New England flora.

The designation "cf.," as used in this paper, indicates some uncertainty about an identification. In these cases the fossils were good matches for reference specimens, but other species in the same genus shared some features with the fossil. In a few cases, all species of a genus had similar seeds, and identifications beyond genus were not possible.

## LATE-PLEISTOCENE PLANT-MACROFOSSIL AND PRESENT FLORAS OF NEW ENGLAND COMPARED

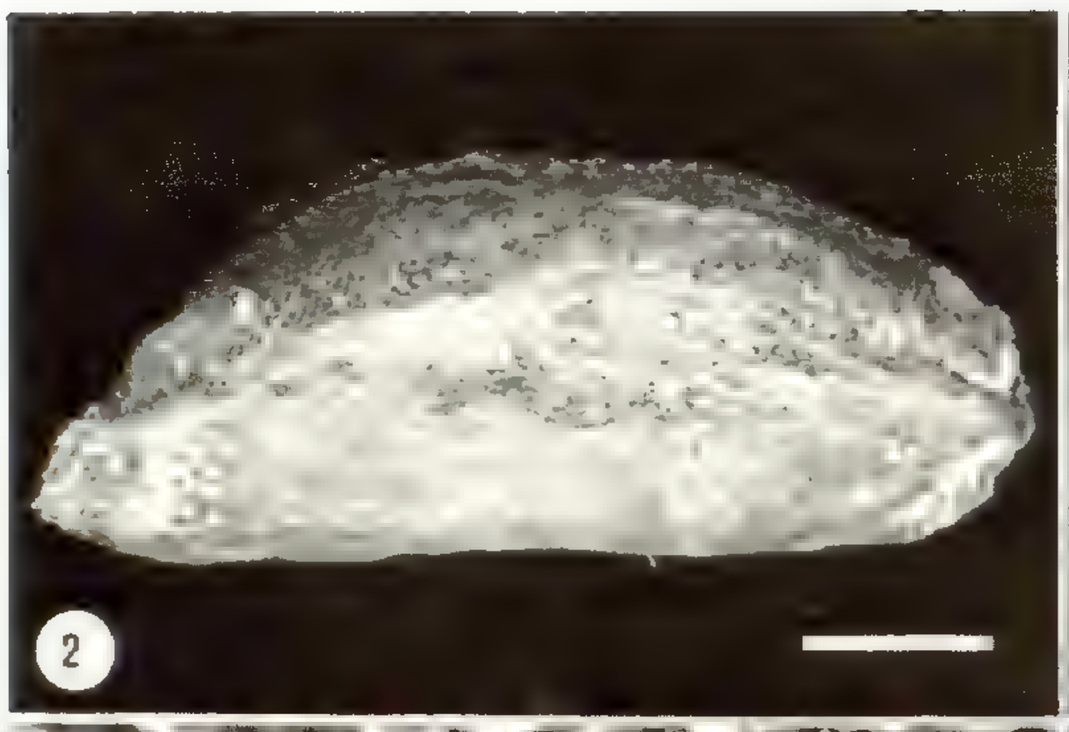
### Tracheophytes

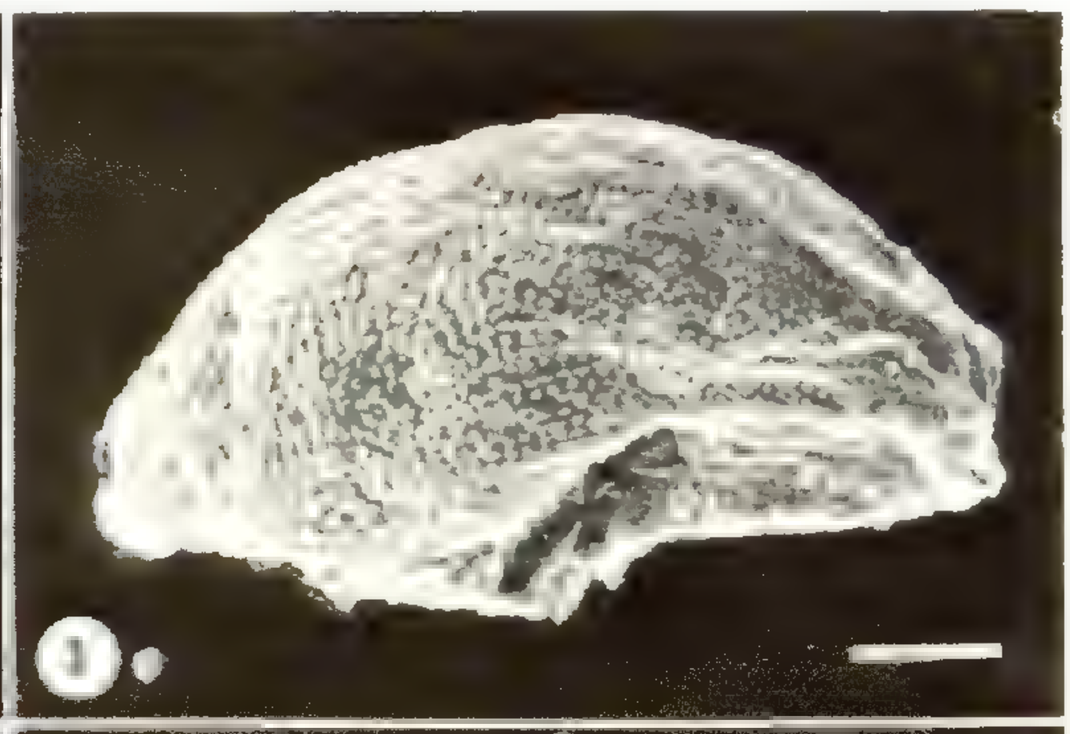
Sediments at Tom Swamp (TS), Columbia Bridge (CB), and Upper South Branch Pond (USBP) produced fossils of 36 different vascular plants, 28 of which were identified firmly to species, six to cf. species determinations, and two to genus only (Table 2). Eight of the 34 species are not known as members of the present flora of New England (Fernald, 1950; Seymour, 1982). However, most of these occur in areas adjacent to the Gulf of St. Lawrence, especially on the Gaspé Peninsula, Québec. The single exception is *Saxifraga* cf. *flagellaris* Willd.[1], a circumarctic species found also as a disjunct in the mountains of the western United States and in Asia (Hultén and Fries, 1986, map 1019). It is represented by subsp. *platysepala* (Trautv.) Porsild in the Canadian Arctic Archipelago and northern and northeastern Greenland. Seeds re-

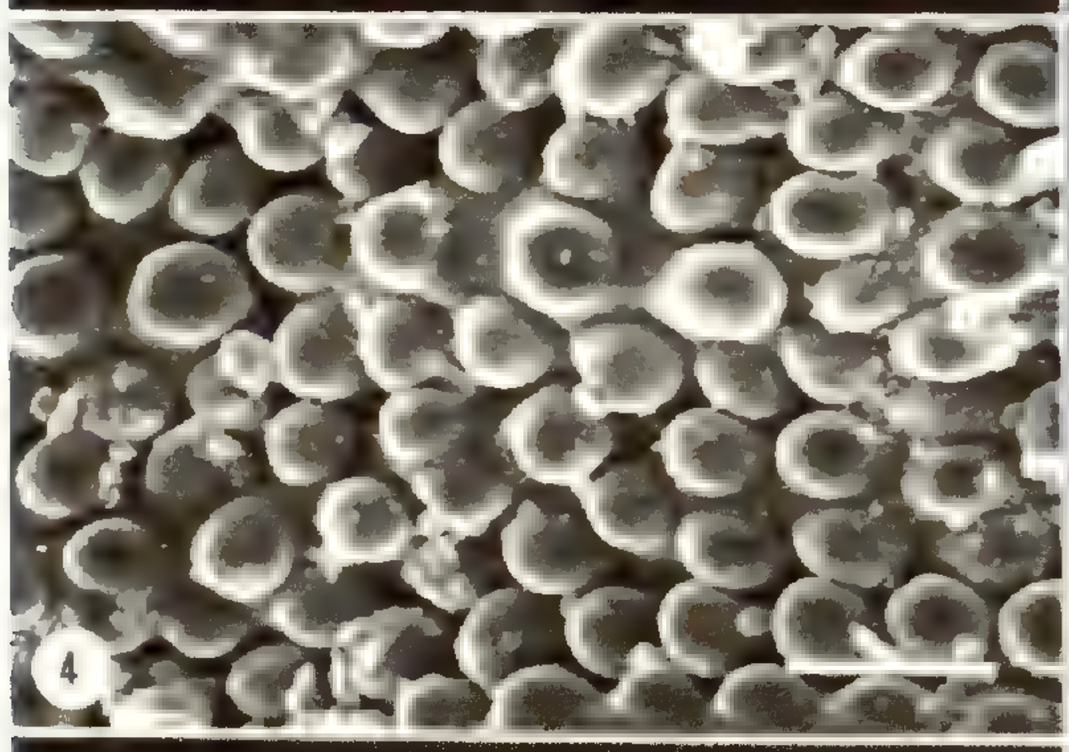
[1] Vascular plant names are mostly those in Fernald (1950). If different, or if a species is not present in the *Gray's Manual* range, authorship is supplied.

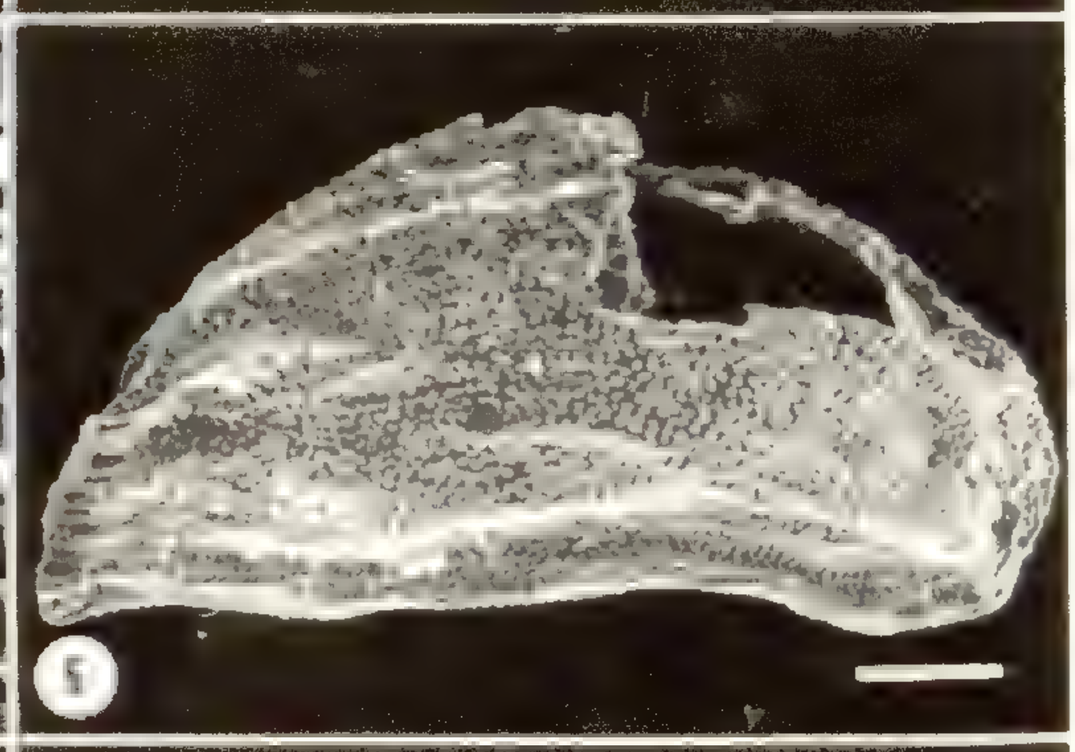
Table 2. Late-Pleistocene tracheophytes of New England based on plant macrofossils. Asterisks (*) denote species that are not present members of the New England flora.

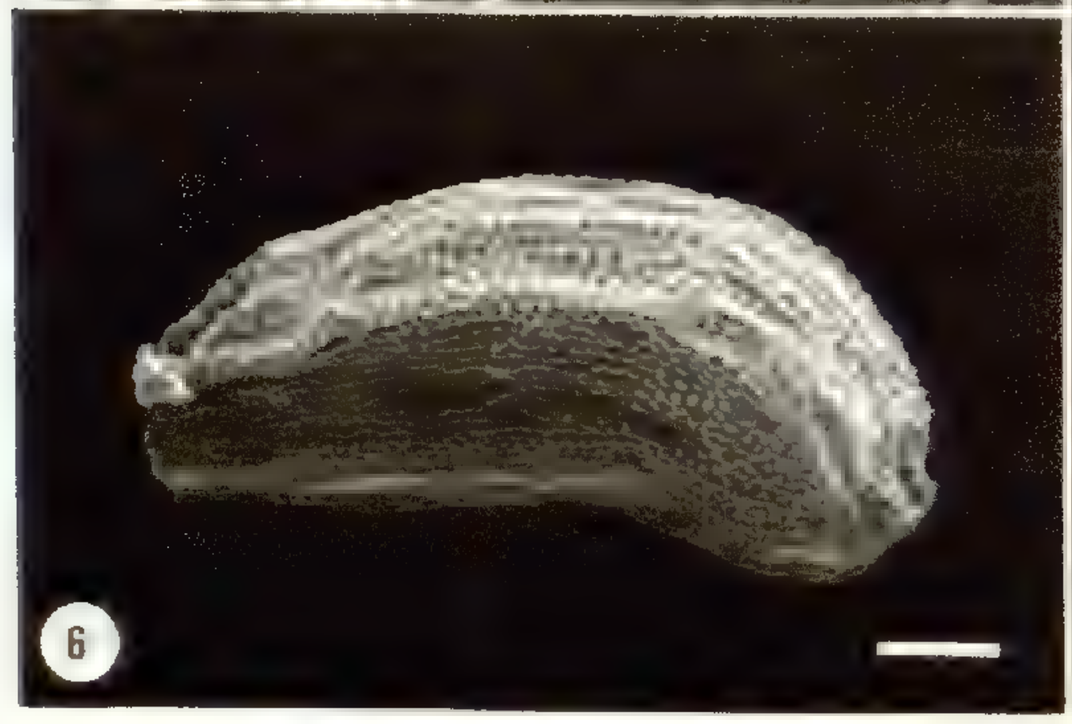
| Species | Tom Swamp | Columbia Bridge | Upper South Branch Pond |
|---|---|---|---|
| *Selaginella selaginoides* | • | + | • |
| *Woodsia ilvensis* | • | + | • |
| *Juniperus communis* | • | + | • |
| *Potamogeton filiformis* | • | + | • |
| *P. pusillus* | • | + | • |
| *Eriophorum alpinum* | + | • | • |
| **Carex bipartita* | • | + | • |
| *C. aquatilis* | • | + | • |
| **Salix vestita* | • | + | • |
| *S. herbacea* | + | + | + |
| *S.* cf. *uva-ursi* | + | + | + |
| *S.* cf. *argyrocarpa* | • | + | • |
| *Populus balsamifera* | • | + | • |
| *Betula* cf. *glandulosa* | • | + | • |
| *Oxyria digyna* | • | + | • |
| *Polygonum ramosissimum* cf. var. *prolificum* Small | • | + | • |
| **Arenaria* cf. *dawsonensis* | • | + | • |
| *Silene acaulis* | + | + | • |
| *Ranunculus cymbalaria* | • | + | • |
| *Draba* sp. | + | + | • |
| **Saxifraga* cf. *flagellaris* | + | • | • |
| *S. aizoides* | • | + | • |
| *S. paniculata* | • | + | • |
| **Parnassia* cf. *kotzebuei* | • | + | • |
| *Sibbaldia procumbens* | • | + | • |
| **Dryas integrifolia* | + | + | + |
| **D. drummondii* | • | + | • |
| *Rubus chamaemorus* | • | • | + |
| **Elaeagnus commutata* | • | + | • |
| *Shepherdia canadensis* | • | + | • |
| *Ledum groenlandicum* | • | + | • |
| *Rhododendron lapponicum* | • | + | • |
| *Harrimanella hypnoides* | + | • | • |
| *Arctostaphylos uva-ursi* | • | + | • |
| *Vaccinium uliginosum* var. *alpinum* | + | + | + |
| *Gentianopsis* sp. | • | + | • |

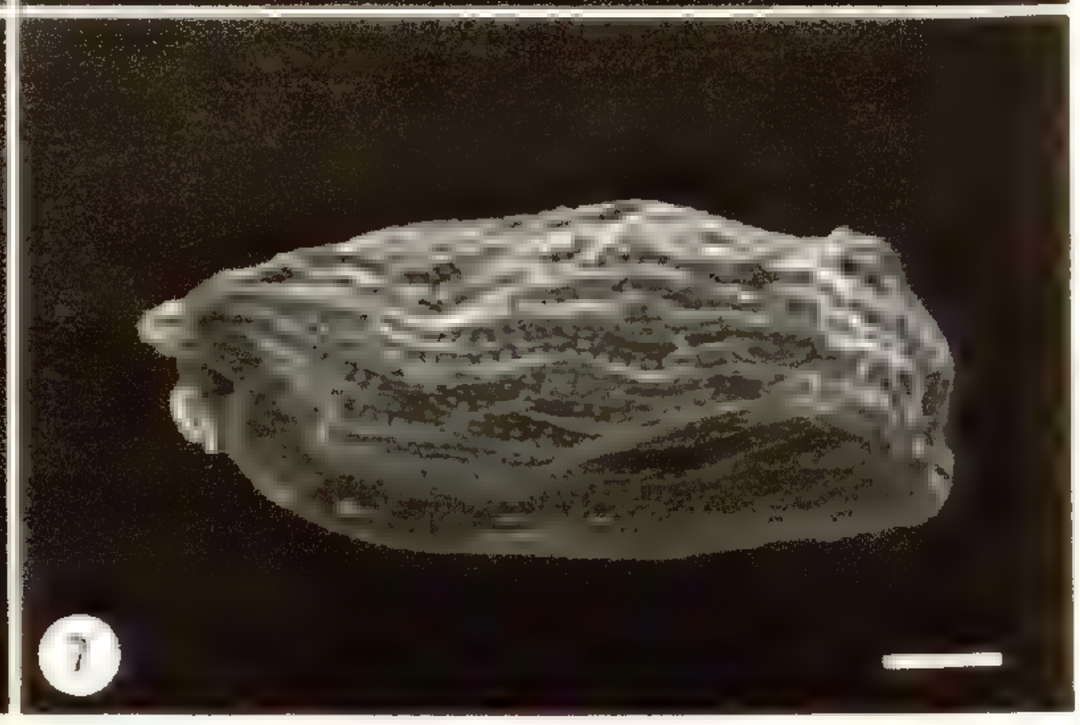


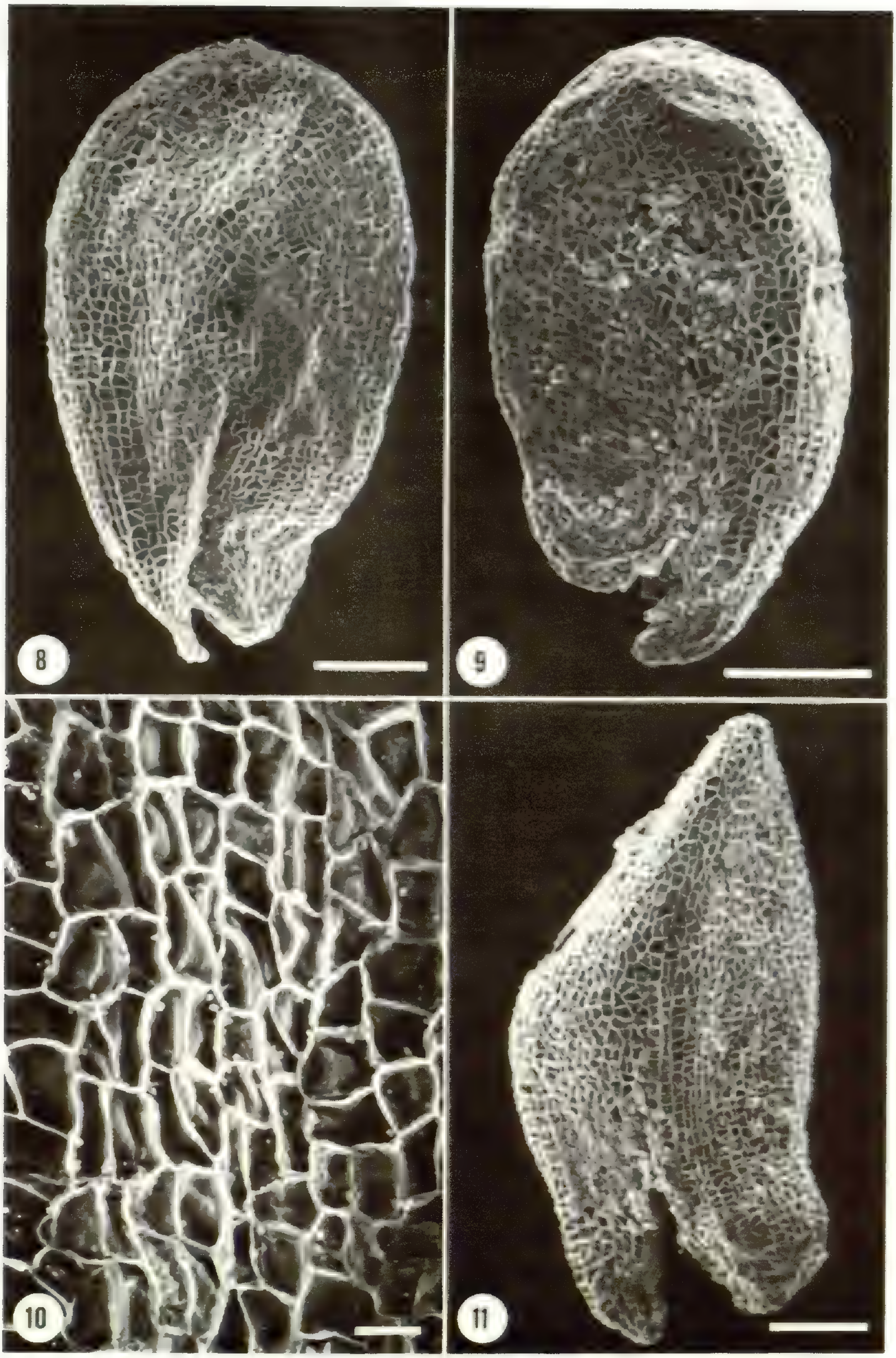



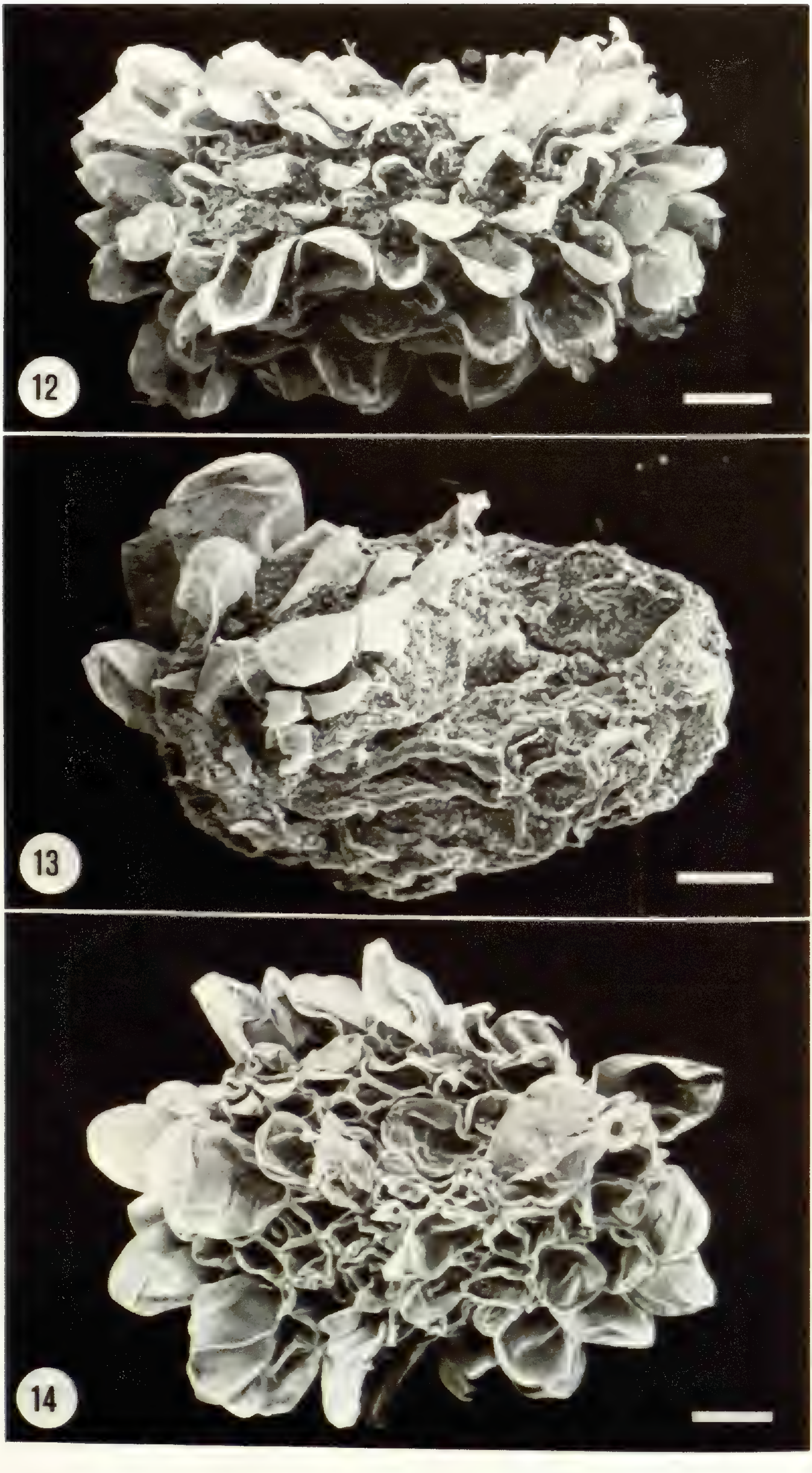

Figures 2–7. Seeds of *Saxifraga*. **2–5.** *S.* cf. *flagellaris,* late-Pleistocene fossils from Tom Swamp, Massachusetts. **4.** Papillose surface of seed (Figure 2) enlarged. **6.** *S. flagellaris* (Canada, N.W.T., e. slope of Richardson Mts., 68°N, 136°W, *Porsild 6828,* 15–17 Aug. 1933 (H)). **7.** *S. cespitosa* (Canada, Québec, Richmond Gulf, e. coast of Hudson Bay, *Abbe et al.,* 1 Aug. 1939 (GH)). Scale bars: 2, 3, 5, 6, 7 = 100 μm; 4 = 10 μm.

ferred to *S. flagellaris* were recovered from TS (Figures 2–5), and while they agreed well with reference specimens in size and general surface microstructure, the density of seed-coat papillae did not match convincingly (cf. Figures 2, 3, 5 with 6). Another saxifrage with papillose seeds, *S. cespitosa,* offered a less satisfactory comparison (Figure 7), and I can find no other acceptable candidates in the North American flora or in Kaplan's exhaustive studies (1981) of seeds of *Saxifraga.*

I have been unable to identify beyond genus probable seeds




Figures 8–11. Late-Pleistocene seeds of *Draba*-type from Tom Swamp, Massachusetts. **10.** Enlargement of surface (Figure 8), outer periclinal cell walls absent. Scale bars: 8, 9, 11 = 100 μm; 10 = 10 μm.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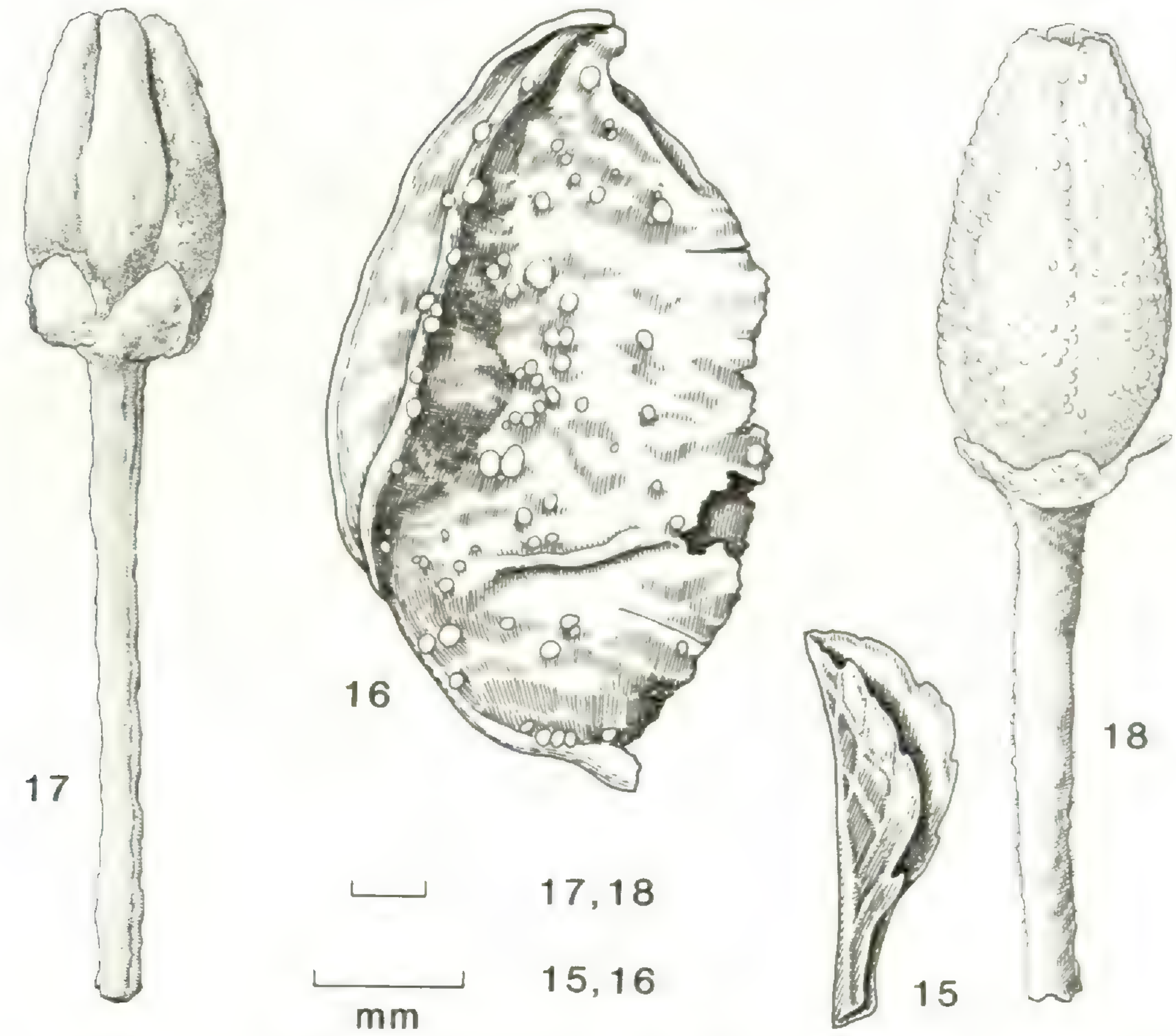
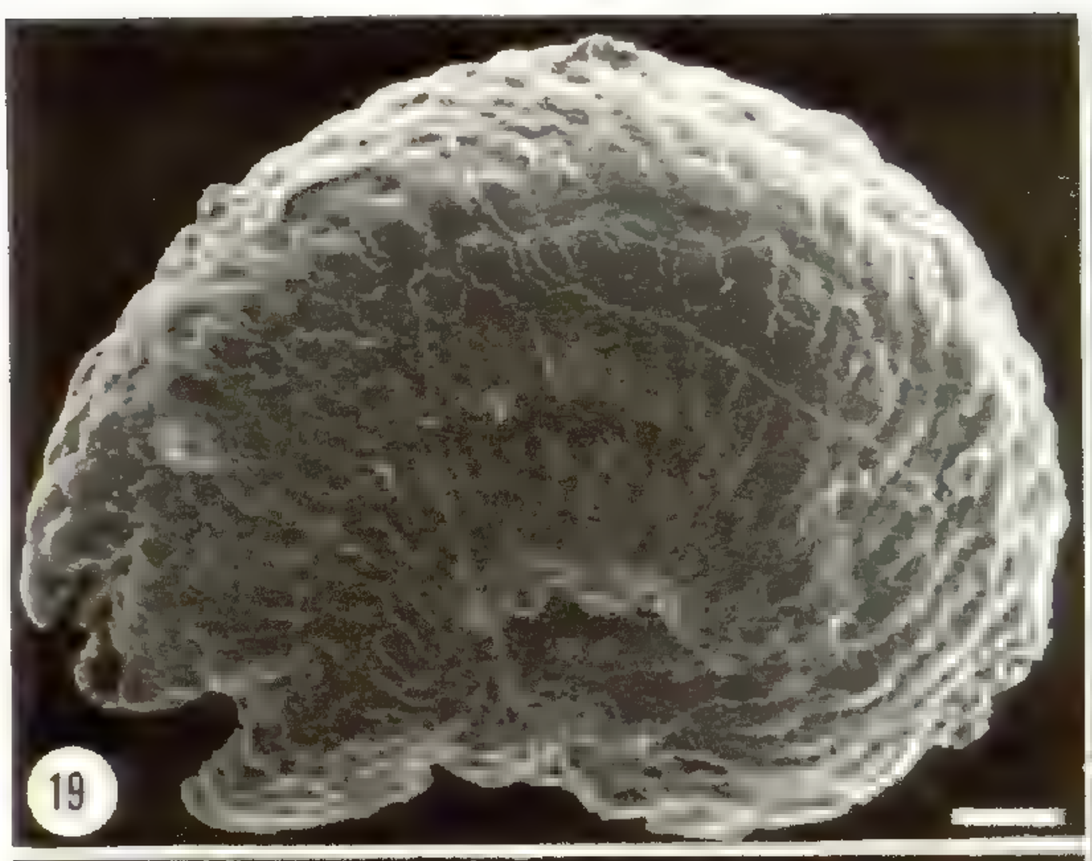


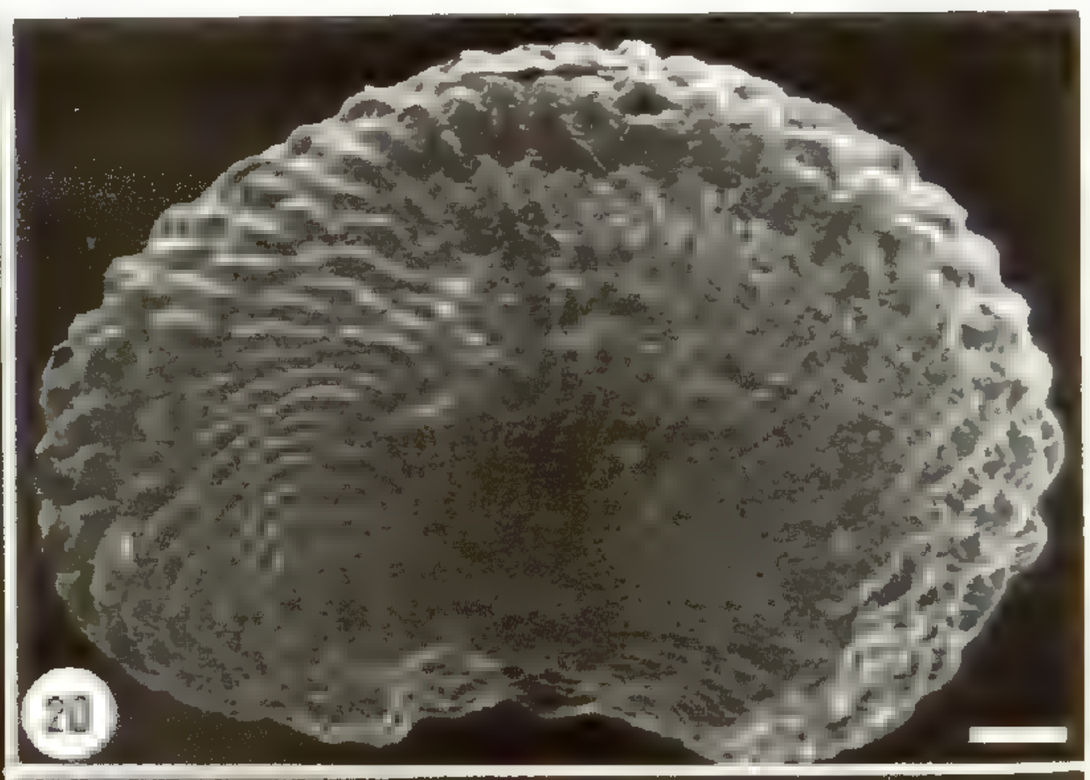

Figures 15–18. Plant macrofossils from the Columbia Bridge Site, Vermont, and a comparative specimen. **15.** Juvenile leaf of *Salix herbacea* (fossil). **16.** Eroded capsule of *Draba* sp. (fossil), replum visible at left; the numerous round structures are fungal fruiting bodies. **17, 18.** Capsules of *Rhododendron lapponicum*. **17.** Fossil. **18.** From herbarium specimen (Canada, w. Newfoundland, North Arm, Bay of Islands, *Long & Fogg 356*, 4 Sept. 1926 (GH)).

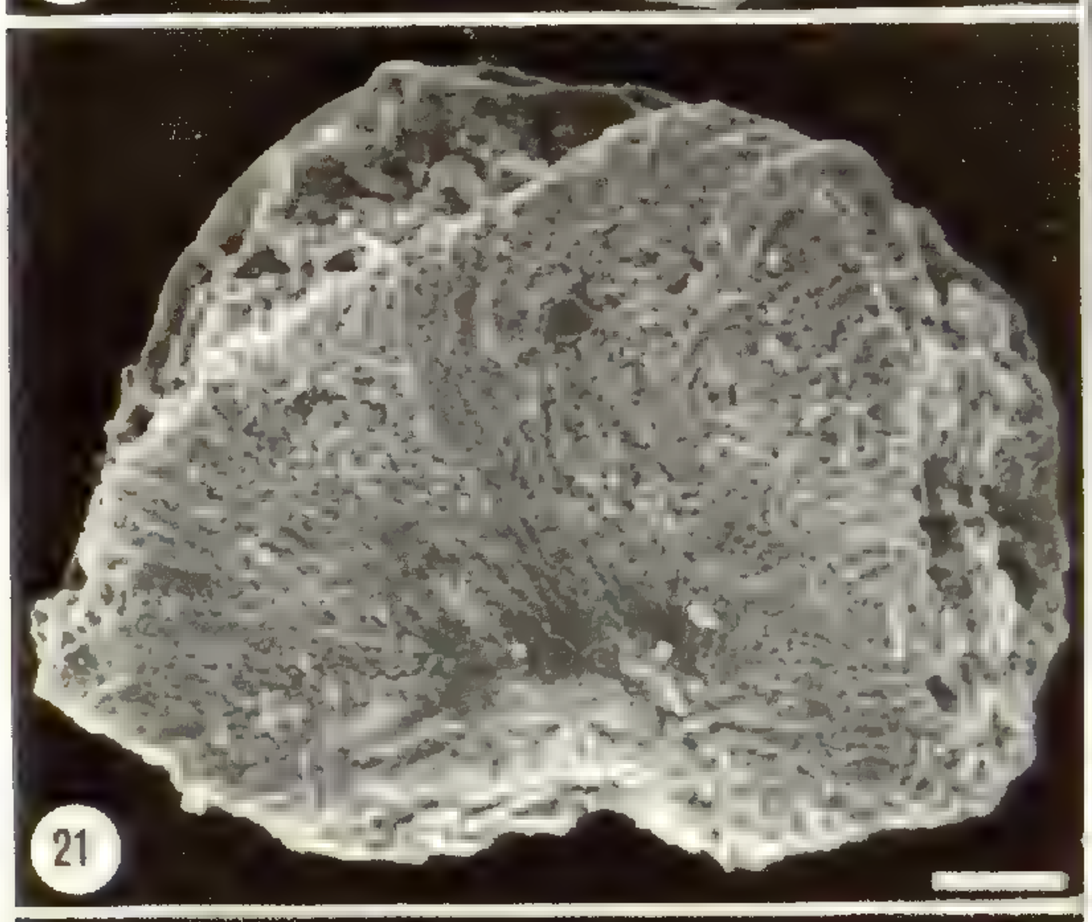
and a fruit of *Draba* (TS, Figures 8–11; CB, Figure 16), a seed of *Gentianopsis* (CB, Figure 12), achenes of *Potentilla* sp. (TS, CB, USBP), seeds of *Arenaria* and Cruciferae and fruits of Gramineae (TS, USBP), achenes of Compositae (TS, CB), seeds of *Juncus*, fruits of *Ranunculus* subg. *Batrachium* and *Carex* spp., and a needle of *Juniperus* (TS), stem fragments of *Equisetum*, recep-

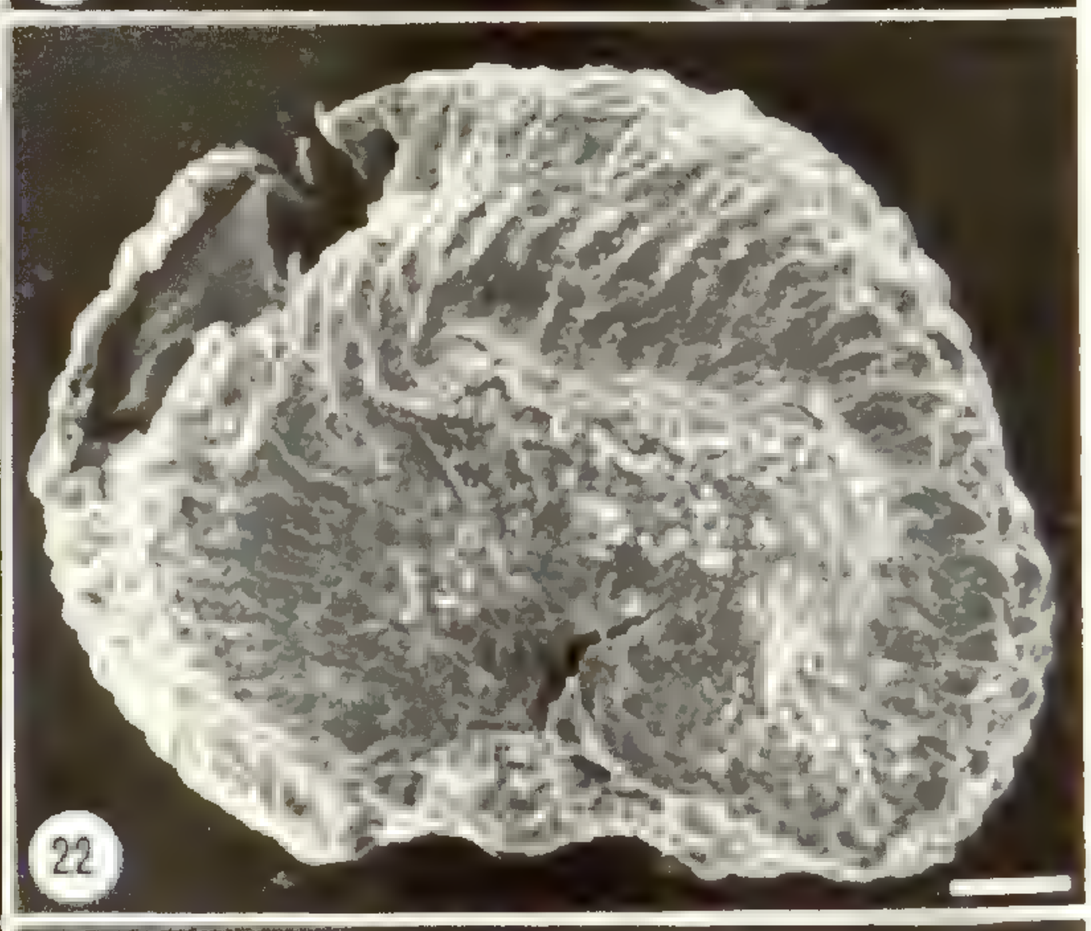
←

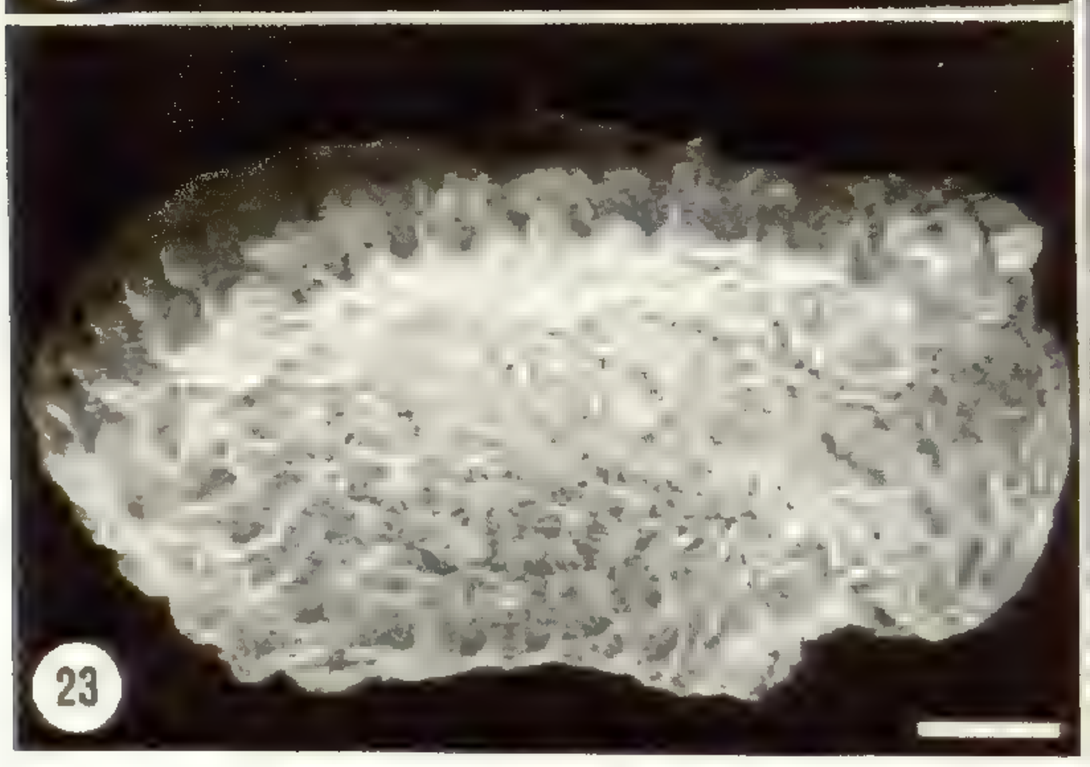
Figures 12–14. Seeds of *Gentianopsis*. **12.** Fossil seed from Columbia Bridge Site, Vermont. **13.** Fossil seed from Brampton Esker Site, Ontario, described in Terasmae and Matthews (1980). **14.** Seed of *Gentianopsis procera* (Canada, Québec, Baie-des-Chaleurs, Rivière Bonaventure, *Marie-Victorin 44573*, 15 Aug. 1931 (GH)). Scale bars = 100 μm.

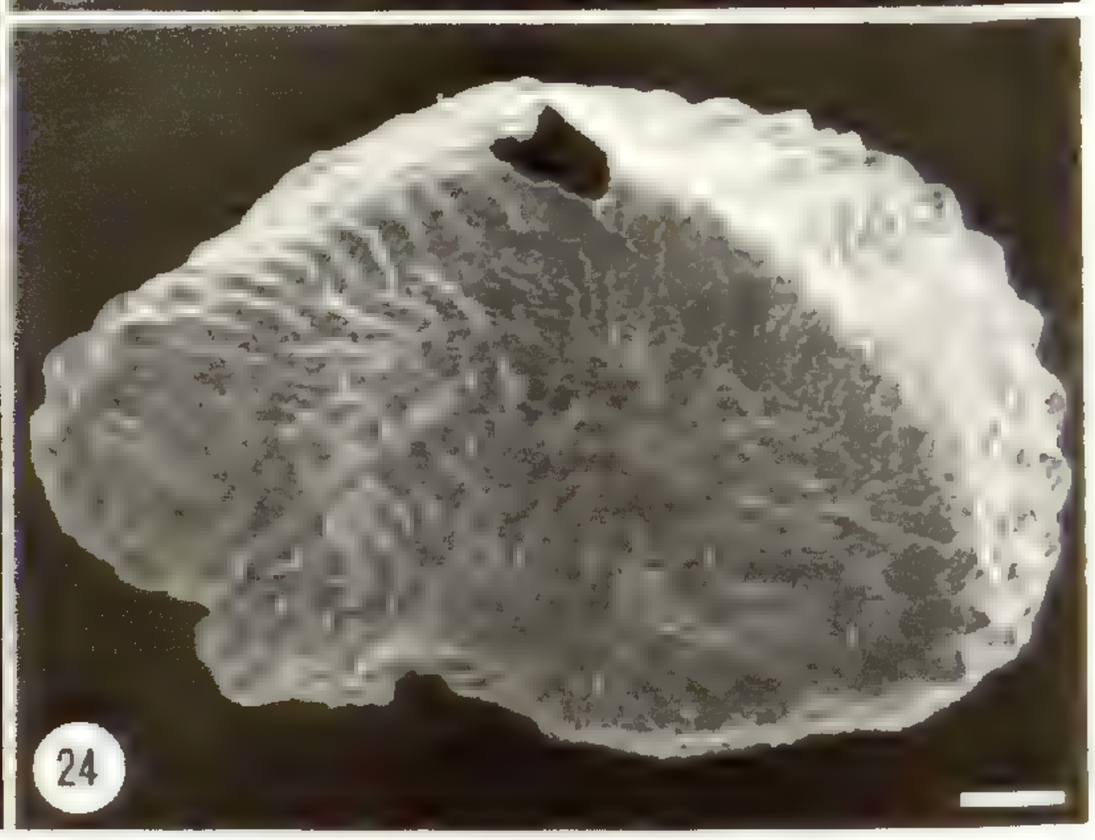


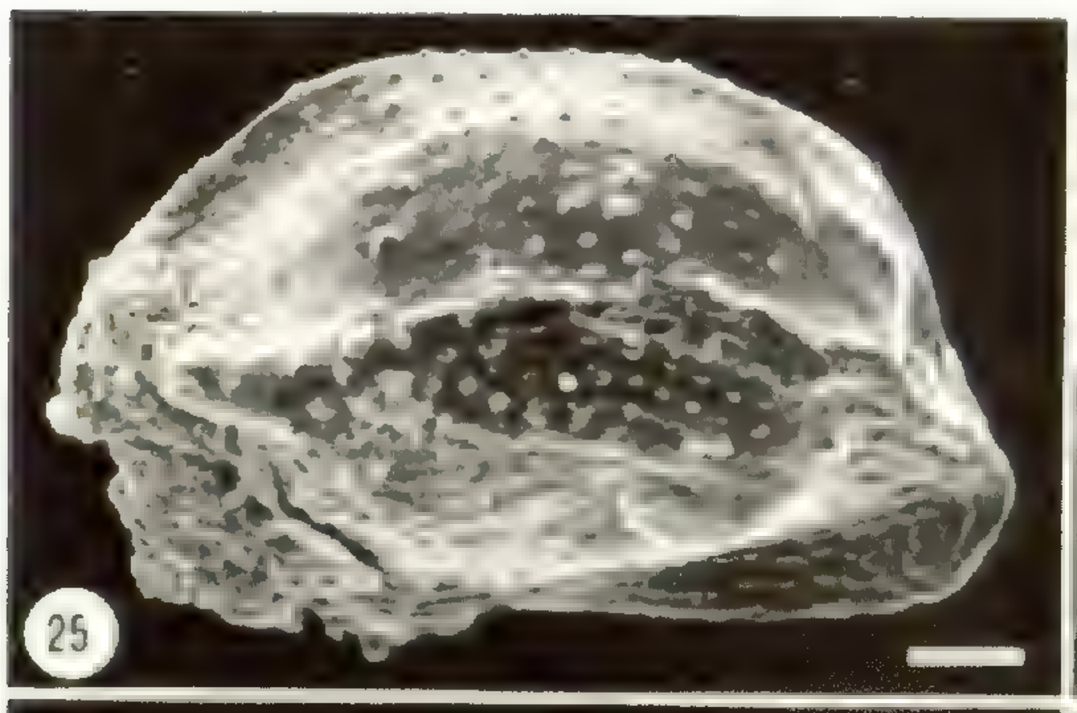



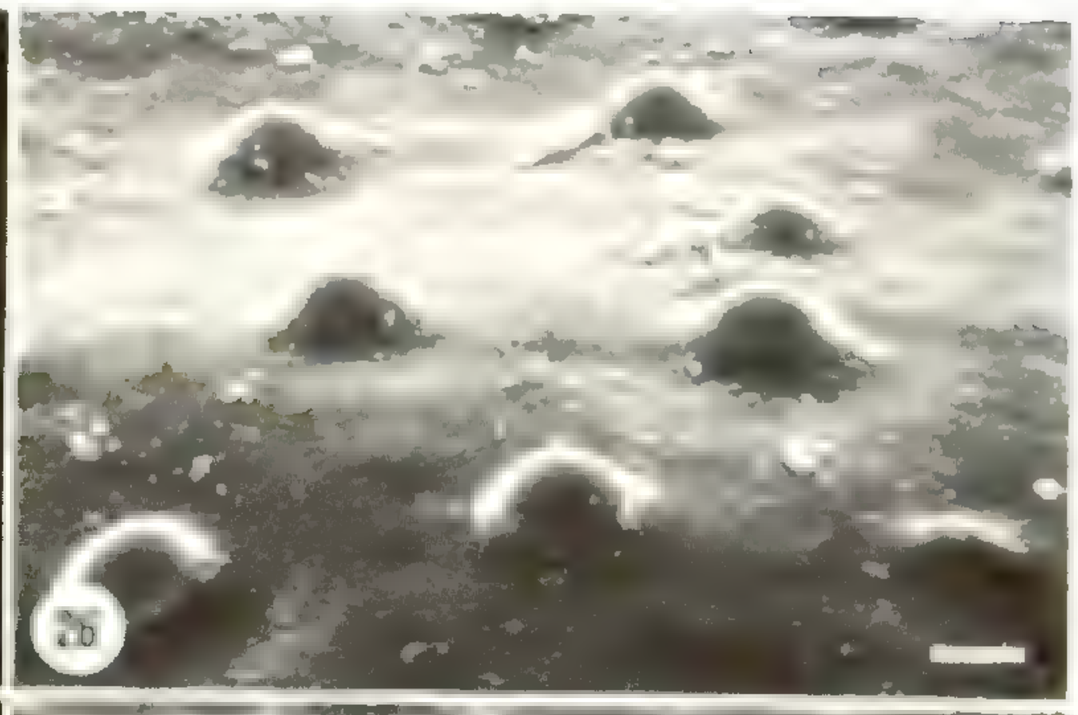



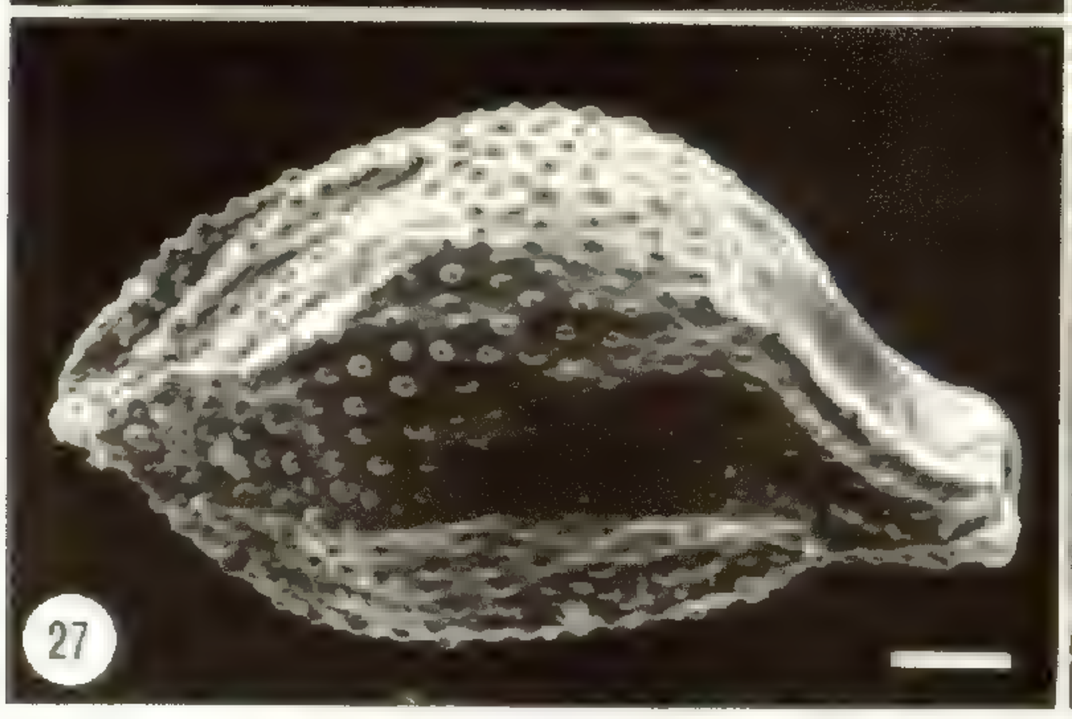

Figures 19–24. Seeds of *Silene acaulis*. **19, 20.** From herbarium specimen (Canada, Québec, Wakeham Bay, Hudson Strait, *Malte 126956,* 24 July 1933 (GH)). **21–23.** Late-Pleistocene fossils from Tom Swamp, Massachusetts. **24.** Late-Pleistocene fossil from Columbia Bridge Site, Vermont. Scale bars = 100 μm.

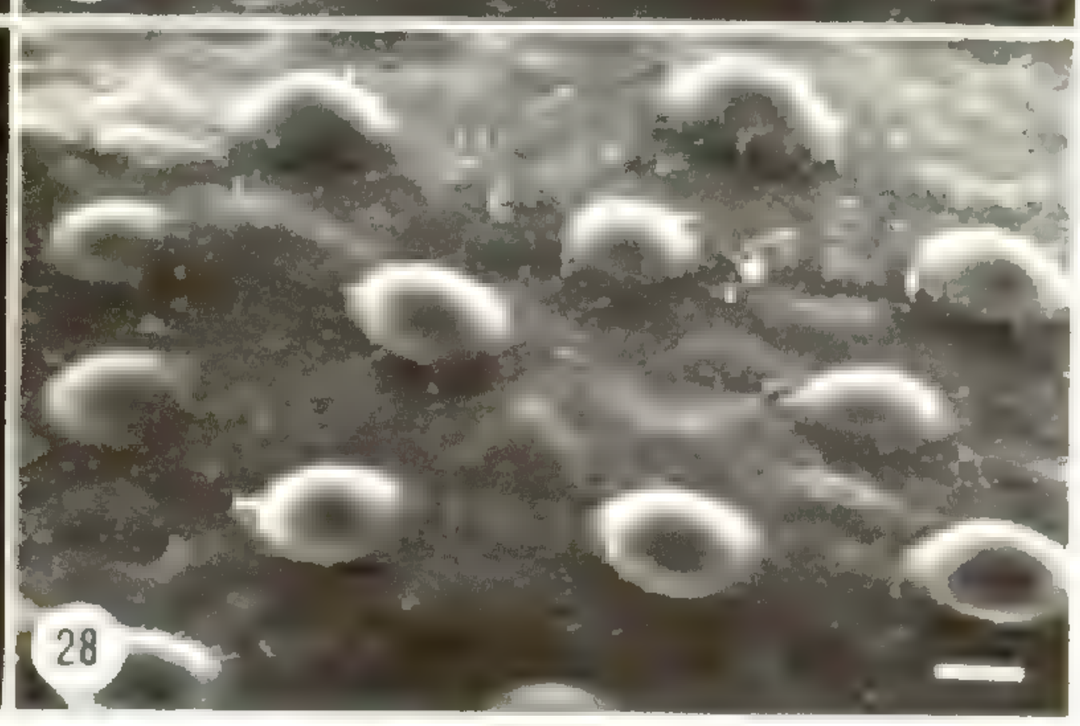
tacles of *Geum* (CB), and fruits of Cyperaceae (USBP). Only a few needles or needle or cone fragments of *Picea* were associated with these fossils at TS and CB.

The present geographical affinities of the plants listed in Table 2 are varied. Some belong to the arctic-alpine element (e.g., *Salix herbacea* (Figure 15), *S.* cf. *uva-ursi, Oxyria digyna, Silene acaulis* (Figures 21–24), *Saxifraga aizoides, S.* cf. *flagellaris* (Figures 2–




Figures 25–28. Seeds of *Saxifraga paniculata*. **25.** Late-Pleistocene fossil from the Columbia Bridge Site, Vermont. **26.** Papillose surface of fossil (Figure 25) enlarged. **27, 28.** Comparative SEM micrographs, seed from herbarium specimen (Canada, Ontario, Thunder Bay District, mouth of Black River, Schreiber, *Hosie et al. 2129*, 21 July 1937 (GH)). Scale bars: 25, 27 = 100 μm; 26, 28 = 10 μm.

5), *S. paniculata* Mill. (*S. aizoon*) (Figures 25, 26), *Sibbaldia procumbens*, *Rhododendron lapponicum* (Figure 17), *Harrimanella hypnoides* (L.) Coville, *Vaccinium uliginosum* var. *alpinum*) and are restricted to present to high-elevation stations in New England or to a few edaphically and microclimatically favorable habitats elsewhere in this region. Others (e.g., *Selaginella selaginoides*, *Eriophorum alpinum* L., *Salix* cf. *argyrocarpa*, *Populus balsamifera*, *Shepherdia canadensis*, *Ledum groenlandicum*, *Arctostaphylos uva-ursi*) are boreal, subarctic, or subalpine in distribution. A third group has a similar northern distribution, but the ranges of the individual species are fragmented into western and eastern North American segments. Examples include *Salix vestita*, *Parnassia* cf. *kotzebuei*, *Dryas drummondii*, and *Elaeagnus commutata*, none of which is presently native to New England.

**Bryophytes**

Associated with fossils of species listed in Table 2 were plant fragments of 66 species of mosses (Miller, 1987a), and nine ad-

Table 3. New England late-Pleistocene moss floras (from Miller, 1987a).

| Site | No. Species | % in Local Flora | % in Regional Flora | % Calcicoles | % Calcicoles in Local Flora | % Calcicoles in Regional Flora |
|---|---|---|---|---|---|---|
| Tom Swamp | 32 | 41 | 75 | 47 | 20 | 60 |
| Columbia Bridge | 45 | 82 | 82 | 71 | 75 | 75 |
| Upper South Branch Pond | 24 | 38 | 75 | 38 | 0 | 22 |

ditional species have been recorded at other sites in New England and nearby Quebec (Mott et al., 1981; Tolonen and Tolonen, 1984). Most of these mosses are presently distributed widely within boreal and subarctic North America, although some have more restricted arctic or arctic-alpine ranges. For a few, the fossils represent occurrences 600–3000 km south of present stations, which are mostly in arctic Canada (Miller, 1987b).

The sizes and some general floristic characteristics of the late Pleistocene moss assemblages at TS, CB, and USBP are summarized in Table 3. In common with moss assemblages of similar age elsewhere in glaciated eastern and northern North America (Miller, 1987a), the three assemblages contain many species that are members of the present local (i.e., within 100 km or less of the sites) or regional (i.e., state) floras. As has been pointed out elsewhere (Miller, 1984), this distribution may indicate that the moss flora of glaciated North America was derived in large part from populations that grew in close association with the fluctuating ice margins rather than from distant sources, for example the southeastern United States.

## PALEOECOLOGY

The three late Pleistocene floras are similar ecologically and consist of mixtures of calcicole and calcifuge species. Edaphic characteristics of New England plants, in particular the correlation between species occurrence and calcareous rock or soil, have been extensively discussed in the pages of *Rhodora,* especially in a paper by Fernald (1907), the autecological investigations of Wherry (1920), and more recent studies. The terms calcicole and calcifuge are used here in the sense of these and other authors as a plant growing on substrata rich in calcium salts or a plant intolerant of calcareous substrata, respectively.

The discovery of fossils of *Dryas integrifolia* and other calcicoles in the oldest sediments of TS and USBP was unexpected because at these sites the local bedrock and soils are acidic. The fossil moss assemblages from TS and USBP (Miller, 1987a) also contained calcicoles, and these fossils indicate the former occurrence of xeric to mesic calcareous rock or soil near both sites and of calcareous (minerotrophic) fens or flushes near TS. The CB fossil flora (both tracheophytes and mosses), which is from an area of calcareous bedrock, was dominated by calcicoles. While this as-

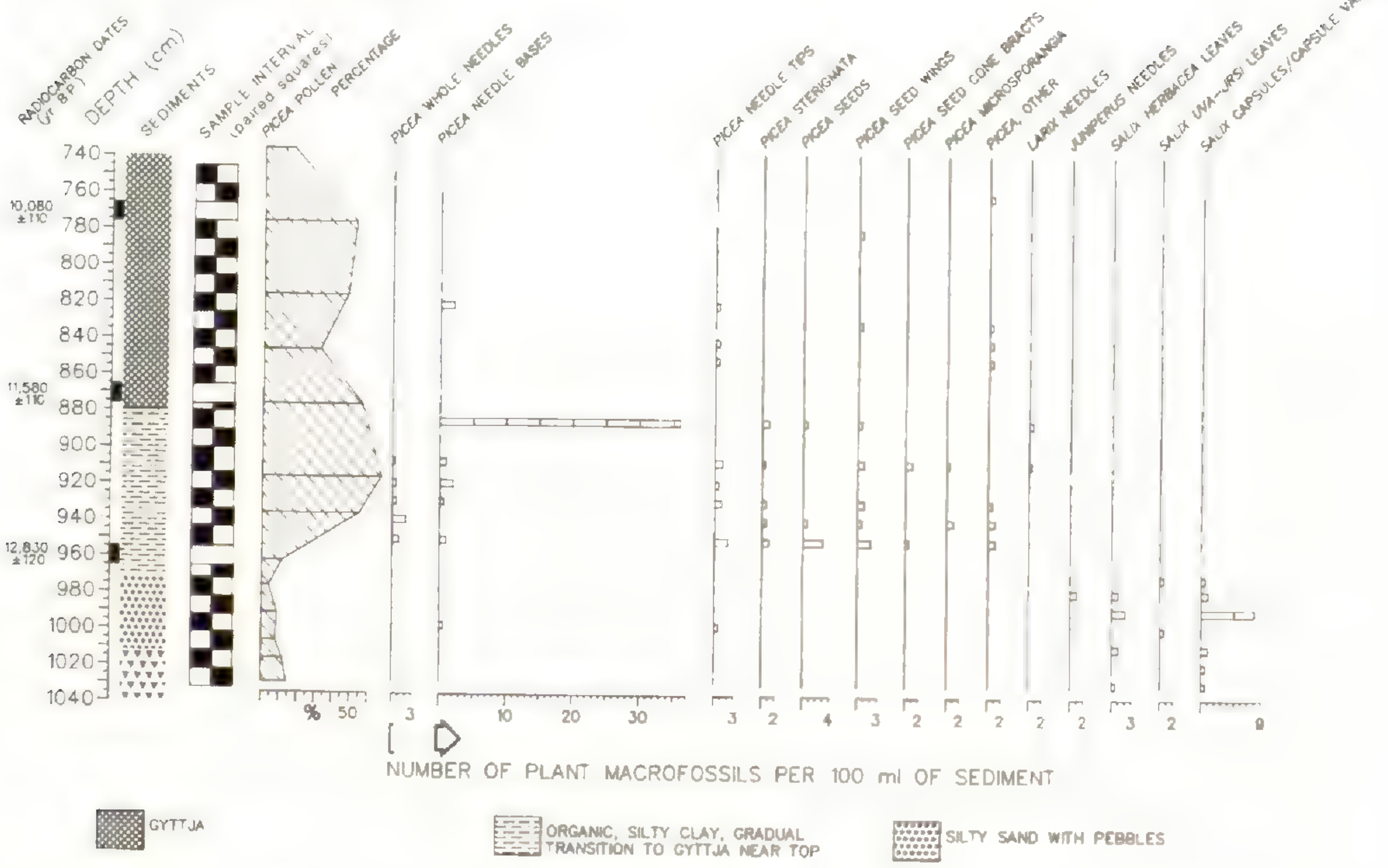



Figure 29. Stratigraphic plant macrofossil diagram for late-Pleistocene and early Holocene sediments at Tom Swamp, Massachusetts. The changing spruce pollen percentages (from Gaudreau, 1986) are included for comparison.

semblage also contained fossils of a few species of acidic habitats (e.g., *Rhododendron lapponicum*), calcifuge species were better represented in the TS and USBP floras.

Many of the tracheophyte and some of the moss species represented in the fossil floras are pioneers that establish on soil that is renewed periodically by erosion or deposition. A few of the tracheophytes (*Dryas* spp., *Elaeagnus commutata, Shepherdia canadensis*) are actinorhizal and are capable of enriching raw mineral soil through the fixation of atmospheric nitrogen.

## SYNTHESIS AND CONCLUSIONS

The surface of New England is a patchwork of acid to circumneutral to somewhat basic habitats that broadly reflect the nature of the local bedrock, glacial drift, or alluvium. The distribution of the vegetation and flora within the region is related, though not determined solely by these edaphic differences, which are also important determinants of plant rarity. For example, the Nashoba Formation of eastern Massachusetts provides small islands of

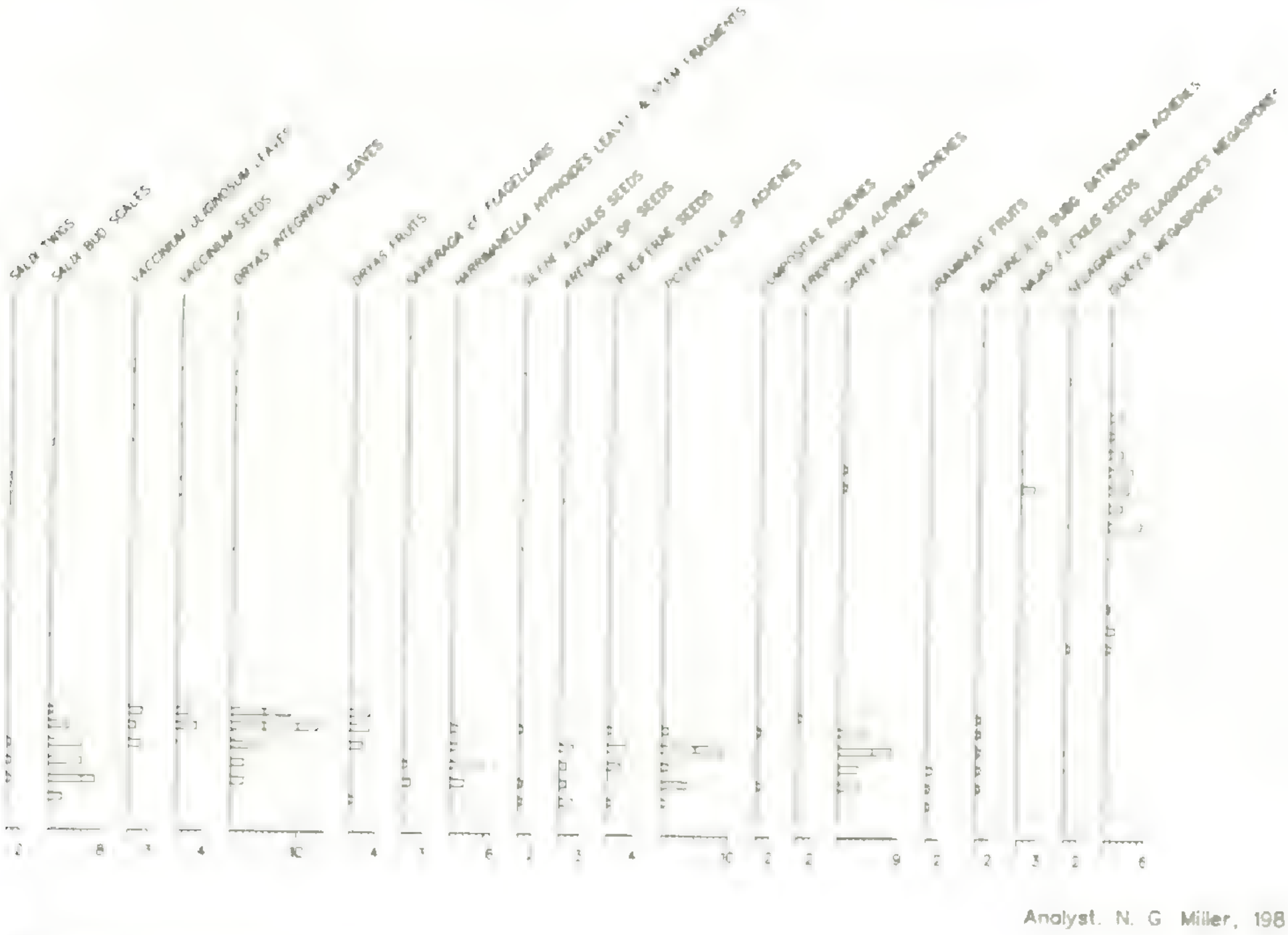



Figure 29. Continued.

calcareous bedrock in a region dominated by acidic soil or rock, and the bryoflora of the Nashoba outcrops includes calcicoles that are otherwise rare or absent in southeastern New England (Mishler and Miller, 1983).

The three late-Pleistocene floras described here indicate that calcareous soils and base-rich wetlands or seeps occurred widely in New England during late-glacial time regardless of whether the fossils were from sites in areas of calcareous or acidic rock or drift. This evidence suggests that calcicoles were once present in many areas where they are now rare or lacking.

The reason for the loss of calcicoles is not known completely. At TS, fragments of arctic-alpine plants (Figure 29) and of calcicole mosses (Miller, 1987a) ceased being deposited at ca. 12,830 ± 120 yr. B.P. with the onset of the regular occurrence of spruce macrofossils and an increase in the percentage of spruce pollen in the stratigraphic record. These changes correlated with an increasing amount of autochthonous organic matter (gyttja) in the sediment and a corresponding reduction in the deposition of inorganic sediment, suggesting that the arrival of spruce somehow

rapidly altered the ground-layer vegetation, possibly through onset of humus accumulation, shading, or other kinds of competitive interactions. The soil may also have become leached of carbonates and certain cations (e.g., $Ca^{2+}$) at this time.

To the north at USBP, parallel stratigraphic changes occurred about 2300 radiocarbon years later. There, the disappearance of calcicoles and arctic-alpine tracheophytes from the record also correlated with the arrival of spruce (based on macrofossil evidence) and with the onset of gyttja deposition. The moss record at USBP documents the transition from late-glacial conditions with fossils of calcicoles to postglacial (Holocene) conditions with fossils of only calcifuge species of mosses.

What are the implications of these temporal and spatial changes for an improved understanding of historical aspects of plant rarity in the New England flora? Arctic-alpine, arctic, subarctic-subalpine, and certain western North American species, including a number of calcicoles, now occur in New England in limited areas of climatically and edaphically suitable habitat. This geographic restriction is in contrast to their occurrence in the late Pleistocene when many of them grew at low elevation sites south of their present range limits. For example, of the 28 species native to New England listed in Table 2, 15 have been designated as rare or endangered in this region by Crow et al. (1981). The loss of these plants from areas of New England that now have acidic soils seems to have occurred at the time of late Pleistocene spruce immigration, which took place time-transgressively in a generally northward direction. I suggest that some species, particularly the calcicoles, may have survived as changing populations through the Holocene at or near stations where they now can be found. At these localities, soil conditions remained appropriate for pioneer species, and competition from trees and shrubs was reduced or absent. However, whether such populations are in fact relicts requires direct evidence, such as that provided by a continuous fossil record beginning in the late Pleistocene. A record of this sort is not now available for any rare species in the New England flora.

The elimination of calcicoles from parts of New England and nearby regions produced fragmented ranges of species that are more widespread in western North America (Miller and Thompson, 1979). This process has left a biogeographical legacy that

may prove important in untangling the taxonomy of difficult species complexes, especially those containing calcicoles. One of these is the genus *Gentianopsis* Ma, which has been studied by Iltis (1965). A seed of *Gentianopsis* was recovered from the Columbia Bridge deposit. Although seeds of species of *Gentianopsis* are similar, the fossil can be referred with some confidence to the *G. procera* (Holm) Ma species-complex, based on the preference of plants of this complex for calcareous soil. The other principal species in eastern North America, *G. crinita* (Froel.) Ma, favors acidic sites.

Iltis (1965) proposed that *Gentianopsis procera* underwent postglacial migration into glaciated eastern North America from a Pleistocene refugium in western North America south of the glacial boundary. However, the fossil record of *Gentianopsis,* which consists of the Columbia Bridge seed and another seed (Figure 13) from late Pleistocene sediments near Brampton, Ontario, establishes that species of *Gentianopsis* grew on recently deglaciated surfaces. This genus and other "western" elements in the flora of eastern North America, such as *Dryas drummondii* and *Elaeagnus commutata,* appear to have been widely established in the East during the late Pleistocene. Although these species now occur mostly in glaciated parts of western North America, they may have been frequent at this time across the continent north of the limit of glaciation when glacier retreat generated appropriate habitats for some few thousand years before the arrival of spruce and other trees. Given the cyclic nature of Pleistocene glacial advances and withdrawals, it is possible that some of these "western" elements may prove to have extensive interstadial histories in eastern North America as well.

The preceding is presented as a framework in which to investigate further some historical aspects of plant rarity in New England. The data reviewed are pertinent especially to arctic-alpine species and northern calcicoles. The history of these elements, as presently understood, may not apply to all calcicoles or to all arctic-alpine species in the New England flora because some species in these categories may have reached New England in the Holocene. Existing data, however, are insufficient to know whether this has indeed happened. Biogeographical problems such as these should be investigated on a case-by-case basis, employing the fossil record whenever possible.

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# PLANT COMMUNITIES OF EASTERN NORTH AMERICA

ARTHUR CRONQUIST

ABSTRACT

Plant communities are human concepts necessary to an understanding of the endless diversity of nature. Some repetitive patterns are evident to all, but an attempt to formalize a classification of plant communities soon leads to debatable choices. Any scheme, including the one I present to you today, must be taken with some reservation.

In Takhtajan's scheme, the plant communities of eastern North America fall into 3 regions. From north to south, these are the Circumboreal Region, the North American Atlantic Region, and the Caribbean Region. In the Circumboreal Region we have the Arctic Province at the north, and the Canadian Province at the south. The Arctic Province is dominated by tundra, and the Canadian Province by boreal, largely coniferous forest, with a frequent admixture of soft-wooded deciduous genera such as *Betula* and *Populus*. Progressively more attenuated fragments of these two northern provinces extend southward as isolated enclaves at progressively higher elevations in the Appalachian Mountains.

Most of eastern United States falls into the North American Atlantic Region, of which the Appalachian Province makes up the largest part. The dominant climax community of the Appalachian Province is deciduous forest, which attains its most favorable development in the moist valleys and slopes of the southern Appalachian Mountains. The two great centers of diversity in this province are in the Southern Appalachian Mountains and the Ozark Mountains. The geologic coastal plain is occupied by the Atlantic and Gulf Coastal Plain Province, in which pine forests and deciduous forests are both well represented. Fire may play a large role in the abundance of the pines. The third province in this region is the North American Prairies Province, mainly of central U.S. and adjacent Canada. The boundary between the prairie and the forest has fluctuated with the climate in post-Pleistocene time, and outliers of the prairie are found as far east as Ohio and central Tennessee.

The essentially tropical Caribbean Region is represented in the United States only by an attenuated fragment of the West Indian Province in southern Florida.

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# ECOLOGY, BIOGEOGRAPHY, AND CONSERVATION OF COASTAL PLAIN PLANTS: SOME GENERAL PRINCIPLES FROM THE STUDY OF NOVA SCOTIAN WETLANDS

PAUL A. KEDDY AND IRENE C. WISHEU

## ABSTRACT

The existence of a coastal plain flora in southwestern Nova Scotia was first documented by Fernald in the 1920's. Recent field work has documented the distributions of coastal plain species more accurately, and there is now a growing emphasis on research dealing with habitat conservation.

Most Atlantic coastal plain plants in Nova Scotia are confined to infertile sand and gravel shorelines on lakeshores where fluctuating water levels prevent shrubs from colonizing the broad, open shorelines. The species are also abundant where exposure to waves is intense. On such shorelines, wave action reduces soil fertility by washing away small soil particles and organic matter. Coastal plain species are very tolerant of such nutrient-poor conditions and can be considered "stress-tolerators." The plants are not abundant at fertile sites apparently because they cannot successfully compete against tall, fast-growing species that normally occur on fertile soil. As a result, the small, slow growing coastal plain plants are restricted to sparsely vegetated shorelines.

Increasing numbers of these species are receiving recognized status from the Nature Conservancy and from the Committee on the Status of Endangered Wildlife in Canada. In spite of this, existing habitat continues to be threatened by cottage development and the use of all-terrain vehicles. The establishment of a conservation strategy to preserve what remains of the flora should include 1) the preservation of whole habitats, 2) consideration of global status of the species, and 3) the incorporation of reserves, buffer zones, and community education and participation.

Key Words: Coastal plain flora, conservation priorities, water level fluctuations, wave exposure, infertility, stress-tolerator, all-terrain vehicles, seed bank

## INTRODUCTION

Our knowledge of the distribution and ecology of coastal plain plants falls neatly into two eras. The first began with the pioneering work of Fernald (1921, 1922) in documenting the existence of these species in Nova Scotia, and ended with the synthesis provided in the Flora of Nova Scotia (Roland and Smith, 1969). These and intervening studies established firmly that southwestern Nova Scotia was botanically distinct from the rest of Canada. A second series of coastal plain communities were documented

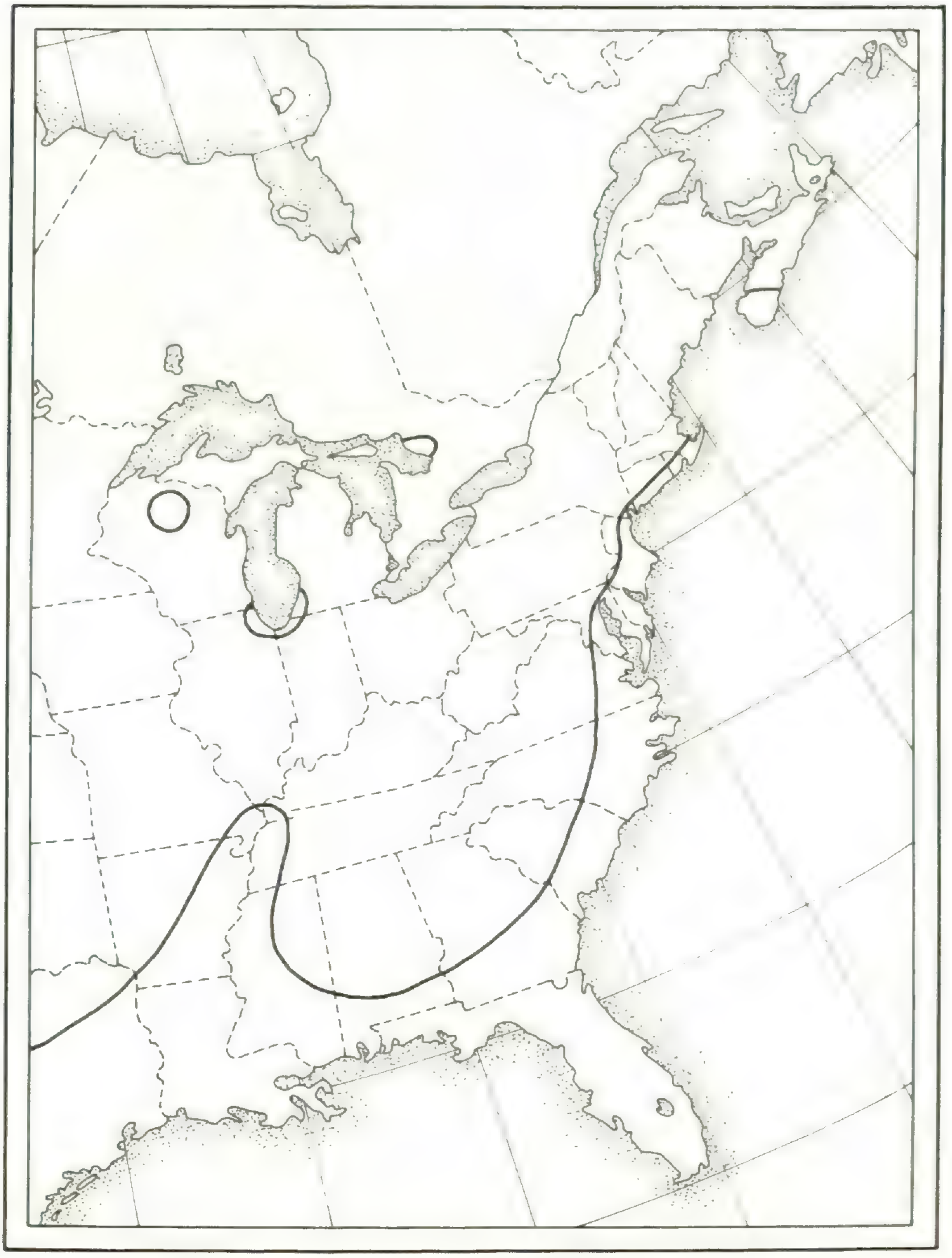

Figure 1. Distribution of Atlantic coastal plain species.

in Canada in the Great Lakes Watershed in the early 1980's (Figure 1; Keddy and Reznicek, 1982; Keddy and Sharp, 1988).

Simultaneously, the second era in our knowledge of coastal plain species began. Emphasis shifted from floristics to ecology and conservation (Keddy, 1985a, 1985b; Wisheu, 1987; Wisheu and Keddy, 1989a). The principal objective of this paper is to

review, using published and previously unpublished data, what we have learned about the ecology and conservation of Atlantic coastal plain floras in the past decade. Although the major emphasis will be upon southwestern Nova Scotia, the region can be thought of as a model system for other coastal plain wetlands.

## BIOGEOGRAPHY

Coastal plain species are believed to have spread to Nova Scotia about 14,000 years ago after the retreat of the Wisconsin glaciation (Roland, unpubl.). The world sea level at that time was over 100 m below the present level and both Browns and Georges Banks were exposed (Figure 2). It is thought that by migrating across this land bridge, species were able to spread northward from the Cape Cod region to Nova Scotia.

The flora occurs within the warmest area of the province, the southwestern edge, with 160–180 frost free days each year (National Atlas of Canada, 1981). Coastal plain species seem restricted by cold temperatures because their numbers diminish as one moves progressively northward (Gleason and Cronquist, 1964). The southwestern region of Nova Scotia is also overlain by sedimentary, rather than metamorphic rock (Figure 3) and it is within the regions of greywacke that the flora is most abundant (Figure 4).

The distributions of coastal plain species within southwestern Nova Scotia follow three patterns. Firstly, there are those species that are relatively widespread, such as *Ilex glabra, Woodwardia areolata, Panicum longifolium,* and *Solidago galetorum* (Figure 4a). They occur throughout the warm region, primarily in the areas with greywacke. A second group of species has a more restricted distribution, but a distribution without an obvious pattern. *Lachnanthes tinctoria,* for example, occurs at only one lake, although it is quite common there. *Clethra alnifolia* is known from only two unconnected lakes and is absent from similar lakes that are nearby. The distribution of *Lophiola americana* also lacks an obvious pattern (Figure 4b). The disjunct nature of this latter group of species suggests that the populations are remnants of once more widespread vegetation (Roland, unpubl.). Since the species are at the northern extentions of their ranges, they may no longer be capable of sexual reproduction, and may therefore be incapable of reestablishing extirpated populations.

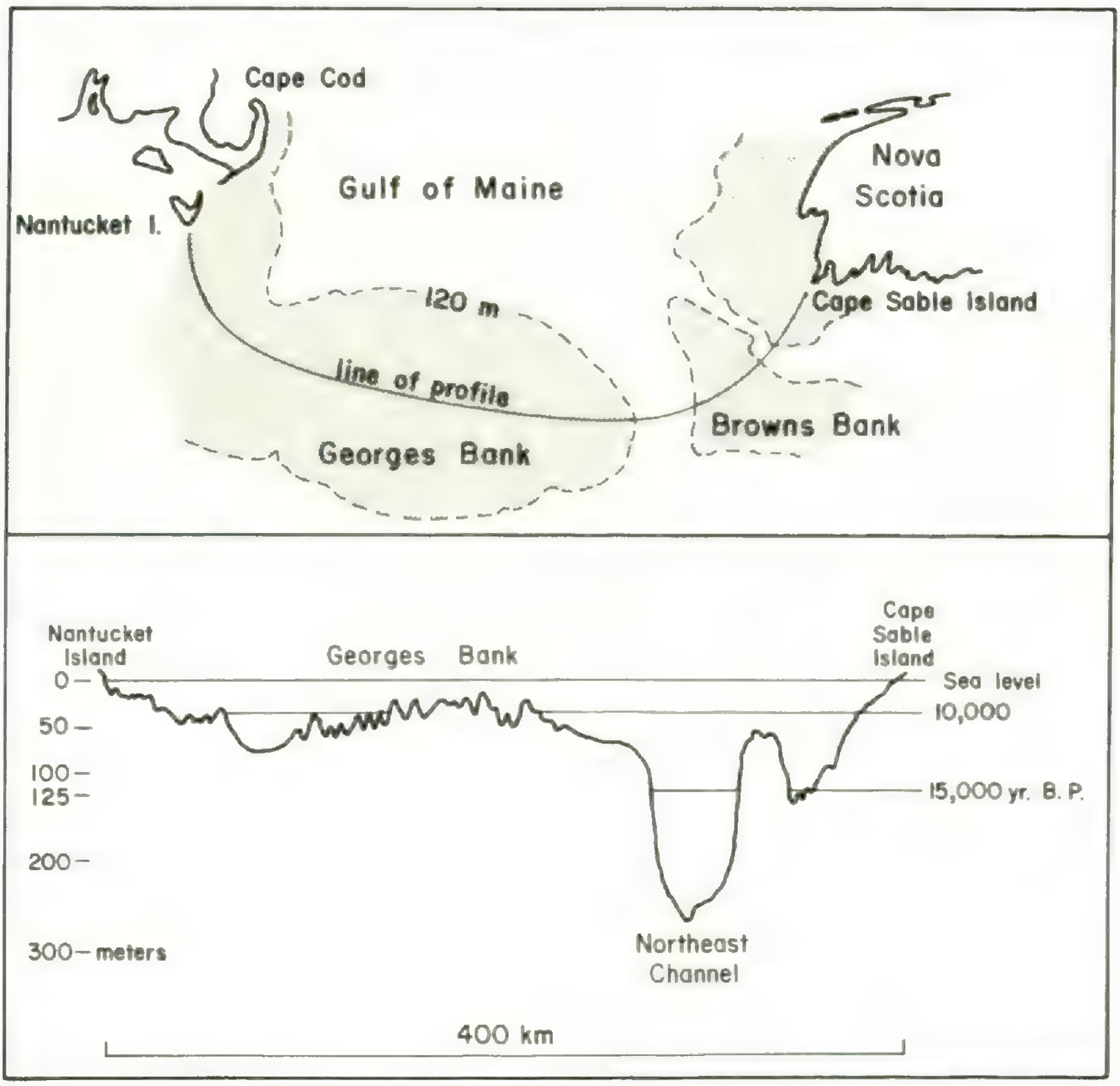


Figure 2. Changes in sea level in relation to a profile from Nantucket Island, Massachusetts, to Cape Sable Island, Nova Scotia (after Ogden and Harvey, 1975).

A third group of species is again quite restricted in distribution, but there is a discernable pattern. Species such as *Coreopsis rosea* and *Sabatia kennedyana* (Figure 4c) are restricted to the Tusket River Valley in Yarmouth County (Keddy, 1985a). These species may be restricted to this one watershed because of their poor dispersal ability or because only in this region are appropriate physical conditions found. Transplant experiments may reveal whether it is dispersal limitations or availability of suitable habitat which produces these patterns.

## ECOLOGY

An initial description of the coastal plain flora concluded that in Nova Scotia, the species are found, almost without exception,

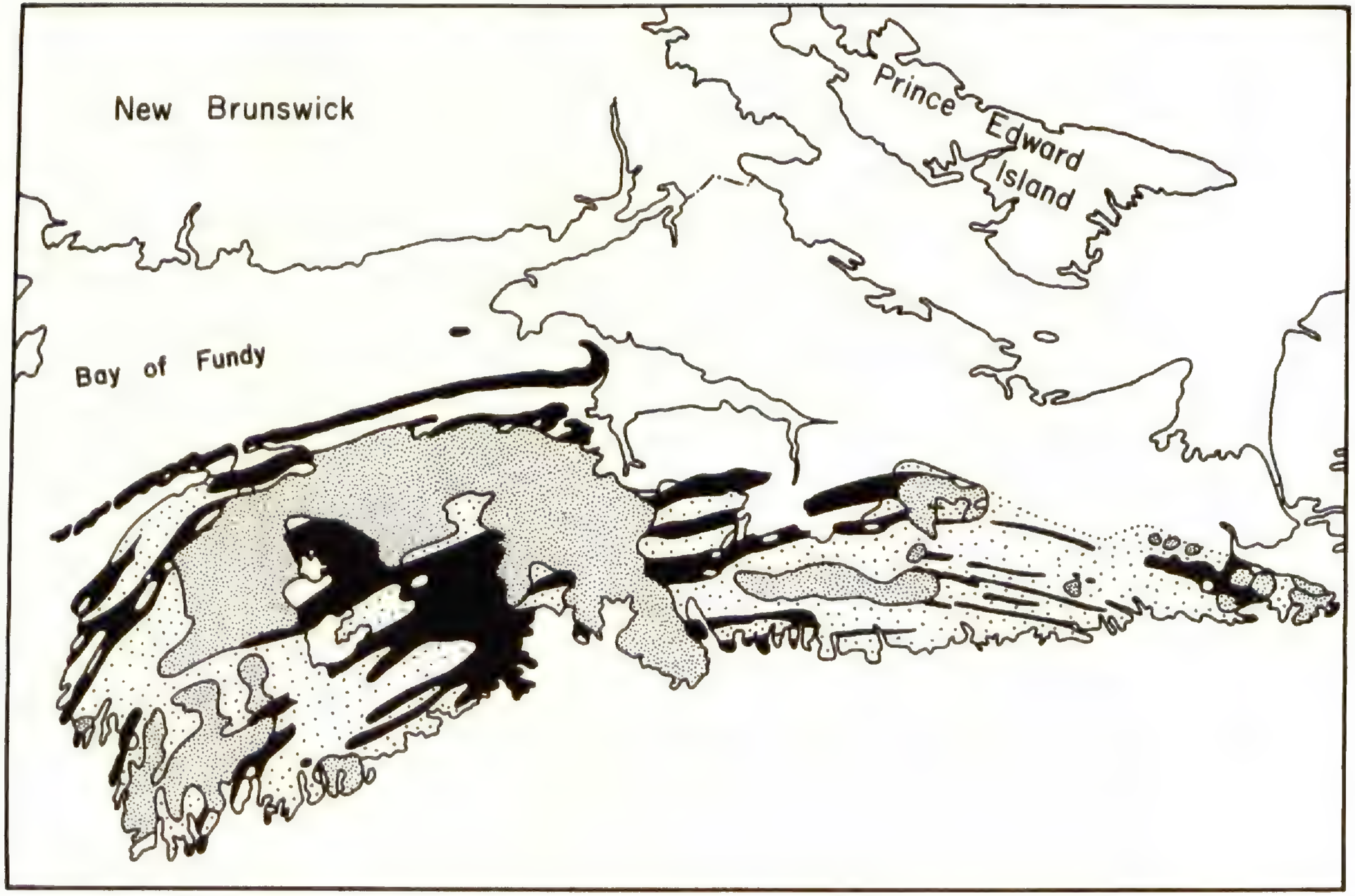


Figure 3. Some rock types found in southwestern Nova Scotia. Slate and North Mountain basalt areas are in black, granite areas are heavily stippled, and greywacke areas are lightly stippled (after Roland, 1982).

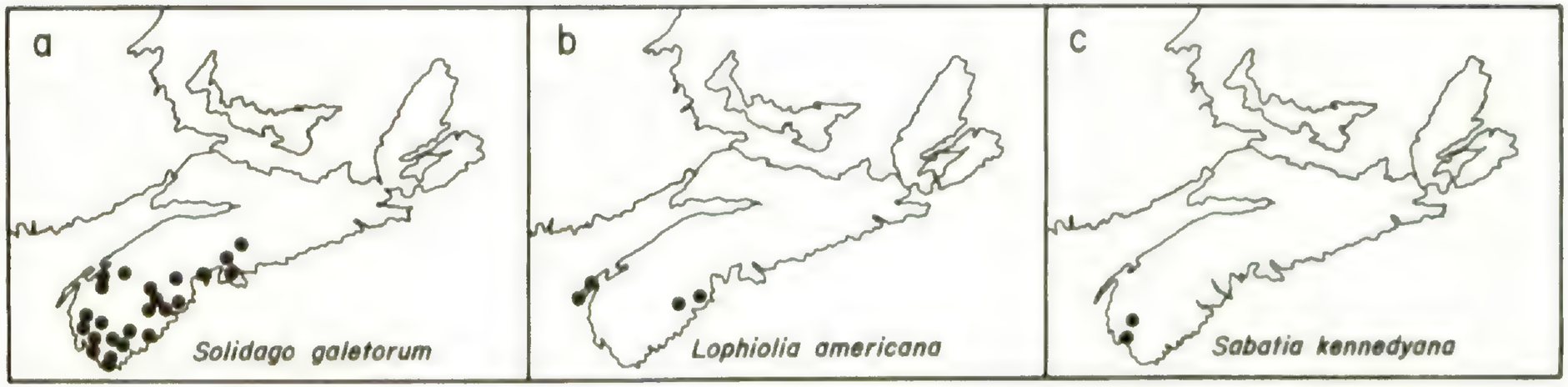


Figure 4. Distributions of selected species in Nova Scotia (after Roland and Smith, 1969).

Table 1. Abundances of Atlantic coastal plain species on lakeshores of different substrate types within the same lake (Wisheu, 1987). Coastal plain species are as in Roland and Smith (1969).

| | Red Till | Local Till |
|---|---|---|
| No. of species | 52 | 57 |
| No. of coastal plain species | 8 | 9 |
| Contribution of coastal plain species to species richness (%) | 15.4 | 15.8 |
| Contribution of coastal plain species to above ground biomass (%) | 23.8 | 9.5 |

in moist or wet freshwater areas (Roland, unpubl.). We have since learned much more about the distributions of these plants and we can now begin to predict at which lakes and where on each lake coastal plain species may be found.

## Among Lake Distributions

As a result of a complex geological history (Grant, 1977, 1980), lakes in southwestern Nova Scotia are of a variety of shapes and sizes and are typically situated on one of two glacial tills. The first till, called "local till" (Grant, 1977), consists of large angular boulders and produces steeply sloping boulder lakeshores. The second "red till" is made up of smooth gravels. It is on the broad, gently sloping shorelines of "red till" that coastal plain species are most abundant (Table 1).

The coastal plain flora is most abundant in lakes which experience large water level fluctuations, such as Kejimkujik Lake (Keddy, 1984a; Roland, unpubl.), Ponhook Lake (Keddy and Wisheu, pers. obs.), and the lakes of the Tusket River system (Keddy, 1985a). Coastal plain plants have been shown to be associated with fluctuating water levels in Ontario as well (Keddy, 1981; Keddy and Reznicek, 1982).

In lakes with frequent fluctuations in water level, shrub growth is inhibited and shorelines remain broad and open (Keddy and Reznicek, 1982, 1986; Keddy, 1985a). Shrubs exclude herbaceous coastal plain species (Keddy, 1983; Sharp and Keddy, 1985). When water level fluctuations are infrequent, shrubs are killed when high water levels return and the herbaceous community has a chance to reestablish from the seed bank. Coastal plain species

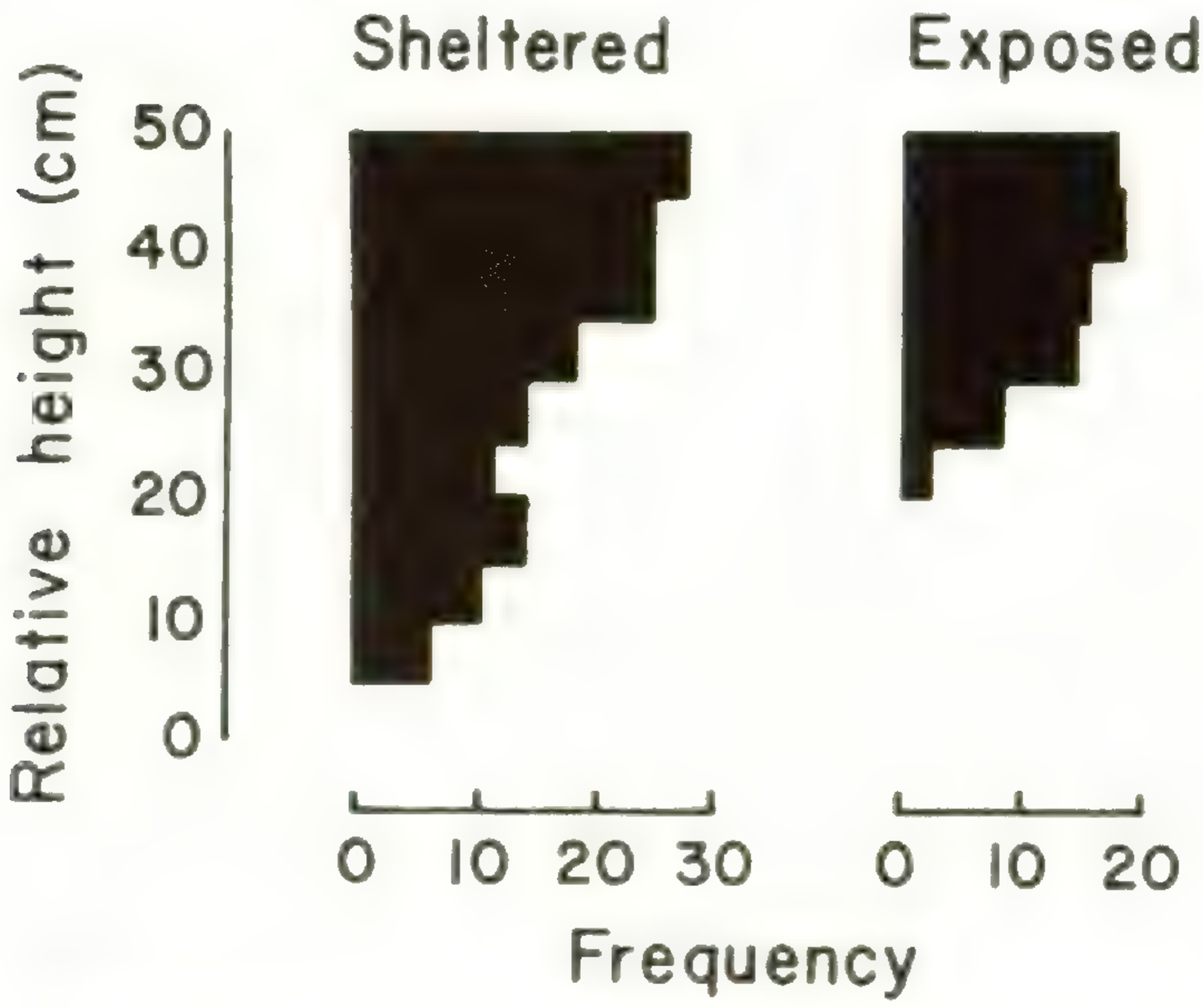


Figure 5. The position of the lower limits of shrubs on exposed and sheltered lakeshores plotted as frequency of shrub species at each elevation summed over ten transects on each shore type. Shrubs occurred more frequently and closer to the water level on sheltered than on exposed shores (after Keddy, 1983).

in Ontario and New Jersey persist in this manner (Keddy and Reznicek, 1982; Nicholson and Keddy, 1983; McCarthy, 1987; Keddy et al., 1989).

The broad, open shorelines suitable for coastal plain plants are also produced by wave exposure. Wave action has two effects. Firstly, at wave-exposed sites, shrubs are prevented from crowding out herbaceous species (Figure 5). Large lakes can therefore support coastal plain species because their exposed shorelines are kept free of shrubs by waves. Waves also inhibit the formation of bogs, a shoreline community in which few coastal plain plants are found (Keddy, 1981).

The second effect of exposure to waves is that the fertility of shorelines is reduced. Wave energy is inversely proportional to organic content (Keddy, 1985b), silt and clay content (Keddy, 1982, 1984b, 1985b), and concentrations of P, K, Mg, and Ca (Keddy, 1985b). The association of coastal plain species with infertile conditions is also indicated by the large number of insectivorous species that grow alongside the coastal plain plants (Moore et al., 1989; Wisheu and Keddy, 1989a, 1989b). The coastal plain species on the New Jersey pine barrens are also growing in soil with low fertility (Gleason and Cronquist, 1964).

## Within Lake Distributions

Since conditions vary along lakeshores, coastal plain plants are not equally abundant on shores even within a single lake. For example, coastal plain plants are most abundant within a zone that is below the shrub line where flooding is frequent (Figure 6). Water depth is a factor known to be important to all shoreline plants (Hutchinson, 1975; Spence, 1982). Other factors that determine the within lake distribution of the species include those which determine among lake distributions: till type and exposure.

On lakes where shorelines include different substrate types, coastal plain species are best represented on the broad, gently sloping "red till" shores (Keddy, 1984b; Wisheu, 1987; Wisheu and Keddy, 1989a). When wave action varies along lake shorelines, the flora is most abundant where exposure is greater (Figure 7). There, the elimination of shrubs and the reduction of fertility create ideal coastal plain habitat.

The effects of infertility and ice and wave disturbance on plant communities can be summarized by a model first proposed by Grime (1973, 1979; Figure 8). This model shows that in areas where stresses (infertility) and disturbances (exposure) are minimal, standing crop and litter is high. Species richness, however, is low in such areas since a few tall, fast-growing species suppress all others. These dominant species lose their competitive superiority in regions which are moderately stressed or disturbed (Grime, 1973, 1979), with the result that maximum species richness occurs in areas of moderate standing crop and litter (Figure 8a). In areas with extreme levels of stress or disturbance, only a few species are able to tolerate the physical environment and both species richness and standing crop and litter are low. It is in these regions of low standing crop and litter than the coastal plain flora is most abundant (Figure 8b; Wisheu, 1987; Moore et al., 1989; Wisheu and Keddy, 1989a).

The mechanisms which restrict species to exposed shores have

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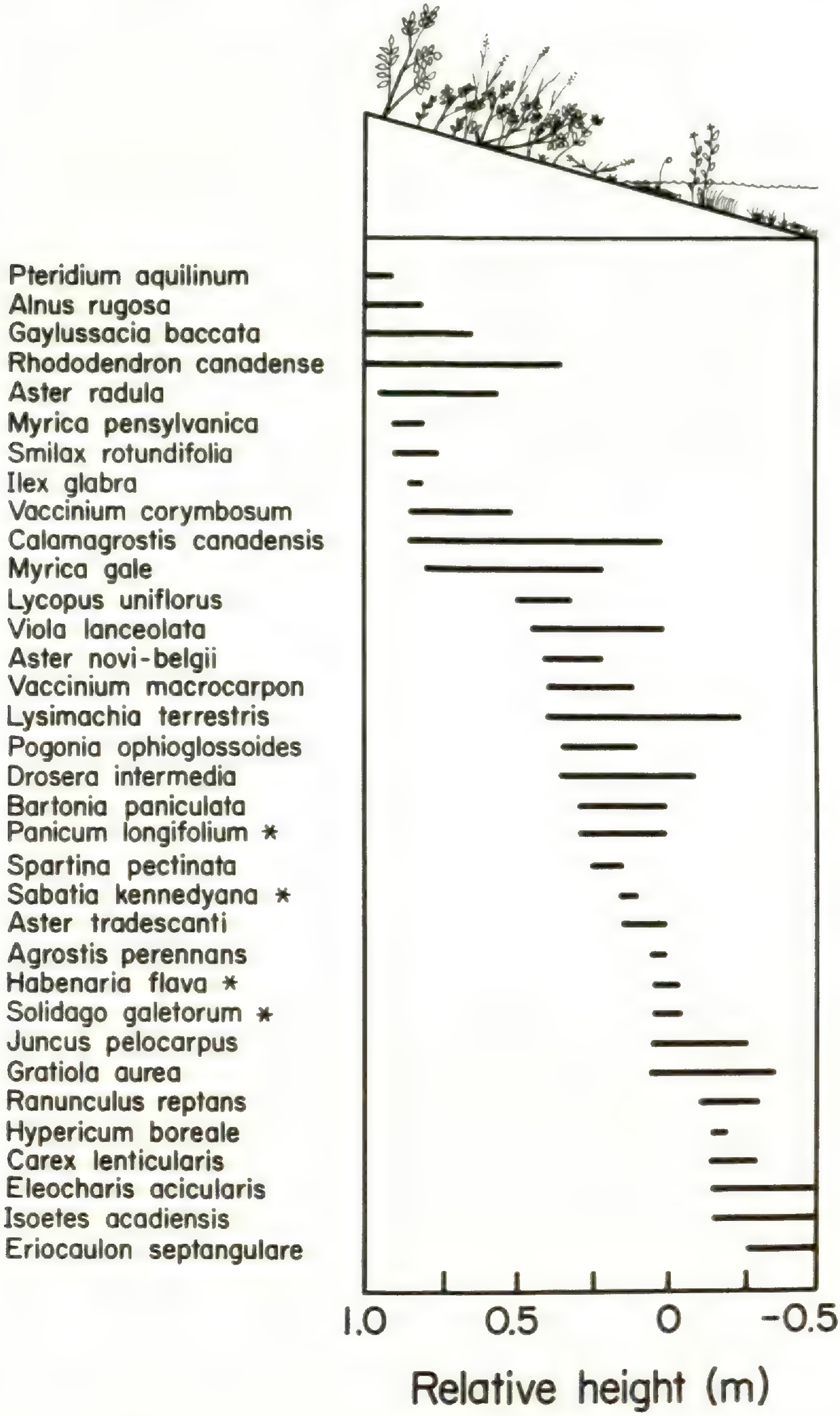
Figure 6. Transect of a typical shoreline on the eastern side of Gillfillan Lake, Nova Scotia (Keddy, 1984a). Asterisks indicate species that are nationally significant (*see* Table 2). (Reproduced with permission from the British Ecological Society.)


Pteridium aquilinum
Alnus rugosa
Gaylussacia baccata
Rhododendron canadense
Aster radula
Myrica pensylvanica
Smilax rotundifolia
Ilex glabra
Vaccinium corymbosum
Calamagrostis canadensis
Myrica gale
Lycopus uniflorus
Viola lanceolata
Aster novi-belgii
Vaccinium macrocarpon
Lysimachia terrestris
Pogonia ophioglossoides
Drosera intermedia
Bartonia paniculata
Panicum longifolium *
Spartina pectinata
Sabatia kennedyana *
Aster tradescanti
Agrostis perennans
Habenaria flava *
Solidago galetorum *
Juncus pelocarpus
Gratiola aurea
Ranunculus reptans
Hypericum boreale
Carex lenticularis
Eleocharis acicularis
Isoetes acadiensis
Eriocaulon septangulare
1.0
0.5
0
-0.5
Relative height (m)

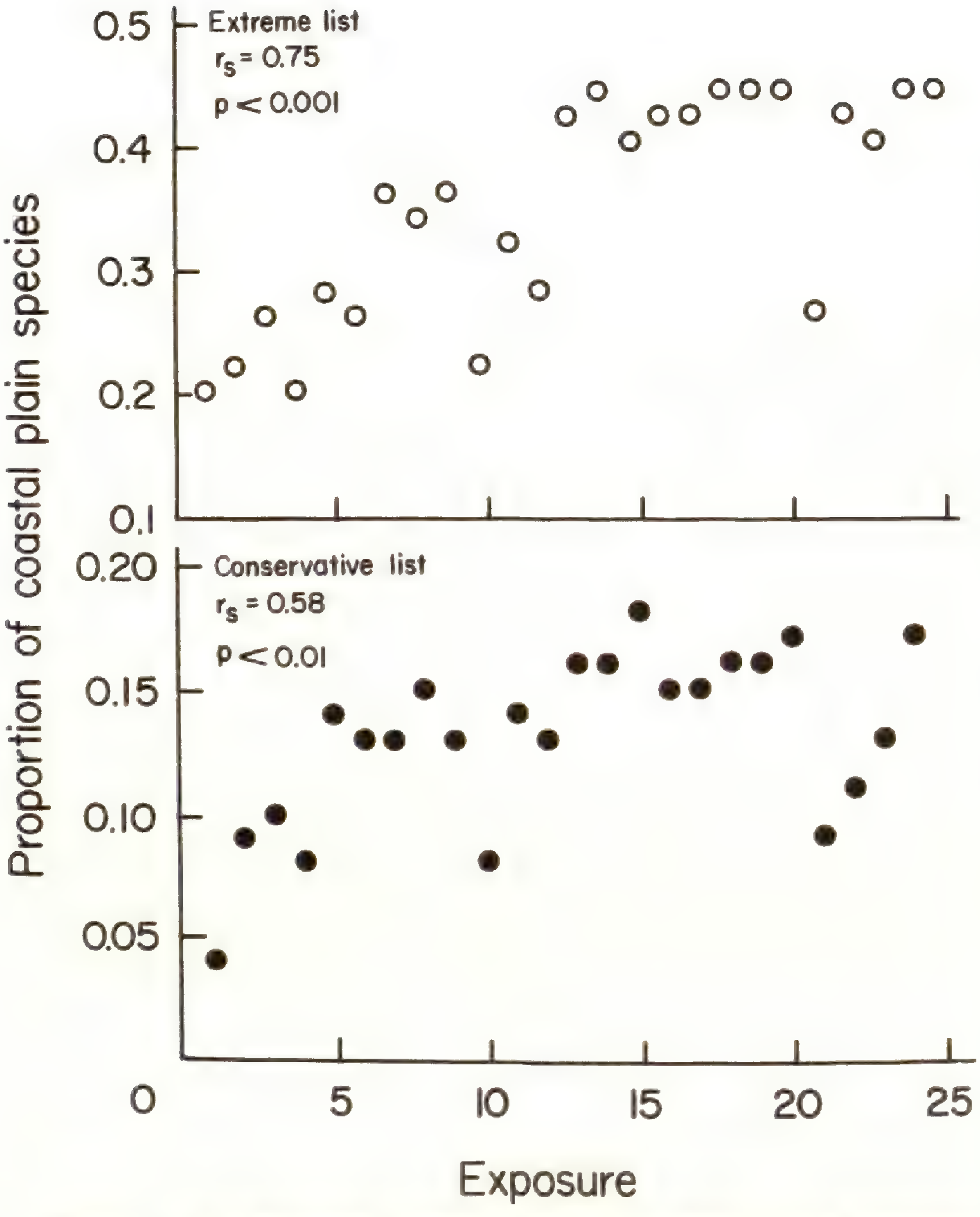



Figure 7. The proportion of Atlantic coastal plain species along an exposure gradient in Axe Lake, Ontario. The conservative list of coastal plain species consists of *Rhexia virginica, Juncus militaris, Nymphoides cordata, Utricularia purpurea, U. resupinata,* and *Xyris difformis.* The extreme list includes *Cladium mariscoides, Drosera intermedia, Juncus pelocarpus, Myriophyllum tenellum, Muhlenbergia uniflora, Potamogeton confervoides, P. oakesianus, U. cornuta,* and *Viola lanceolata.* Nomenclature follows Gleason and Cronquist (1963) except for *Xyris difformis* Chapman. "$r_s$" indicates the Spearman rank correlation coefficient (Keddy, 1985b). (Reproduced with permission from the *Canadian Journal of Botany.*)

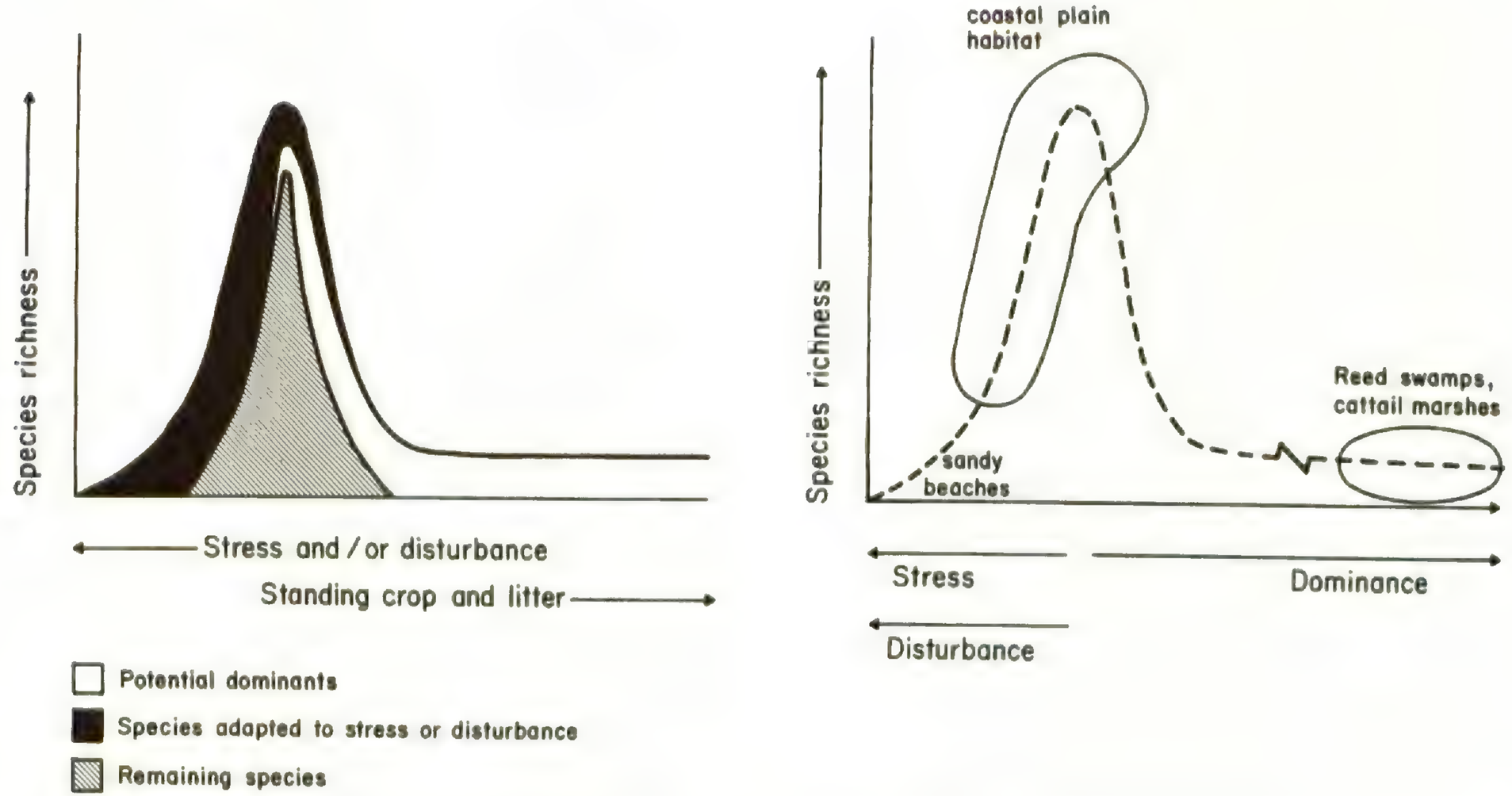



Figure 8. Model summarizing the effect of stress and disturbance on species richness, species distributions, and standing crop and litter. The left figure is from Grime (1973, 1979) and the right relates it to our current understanding of shorelines and coastal plain habitat.

been the object of extensive experimental studies. Wilson and Keddy (1985) recreated the lakeshore soil gradient in pots and showed that species with different field distributions tended to all show best growth in substrate from sheltered bays, suggesting that these species had inclusive niche structure or "shared preferences" along this gradient. A transplant experiment lasting two growing seasons (Wilson and Keddy, 1988) showed that both survival and growth rates decreased with increasing exposure. Grime (1973, 1977, 1979) predicted that stress-tolerators were poor competitors, and more recent experiments confirm this. Wilson and Keddy (1986a) showed that competition intensity increased from infertile beaches to sheltered bays. Moreover, those species with the weakest competitive ability were restricted to infertile beaches (Wilson and Keddy, 1986b)—the habitat with the lowest competition intensity. Gaudet and Keddy (1988) screened forty-four wetland plant species for competitive ability and found that the small partially evergreen species were, in general, poor competitors. The two coastal plain species in the experiment (*Sabatia kennedyana* and *Panicum longifolium*) both had weak competitive ability relative to other more widespread shoreline species (e.g., *Lythrum salicaria, Bidens cernua,* and *Typha latifolia*). This accumulated evidence suggests that coastal plain species occupy habitats which strong competitors cannot invade.

Many members of the coastal plain flora occupying these habitats are small, slow-growing species with rosette growth forms and with evergreen tissue (Wisheu, 1987, 1989b). These traits are associated with the stress-tolerator strategy (Grime, 1977); Greenslade (1983) and Southwood (1988) call such species "adversity selected." Their growth form is similar to the "isoetid" (Hutchinson, 1975), a group of aquatic species considered to be "stress-tolerators" (Boston, 1986; Boston and Adams, 1987; Wisheu and Keddy, 1989a, 1989b). The similarity of coastal plain species to isoetids also shows up in their distributions along the standing crop gradient (Figure 9).

Superimposed upon the effect of standing crop is the effect of peat accumulation. Our field observations suggest that on wave exposed shorelines, a cyclical succession occurs: vegetation cover increases in large stands of *Cladium mariscoides* and then declines when the *C. mariscoides* is eroded away (Figure 10). In recently scoured or disturbed areas, species such as *Lobelia dortmanna* and *Hydrocotyle umbellata* occur on the exposed sand and gravel

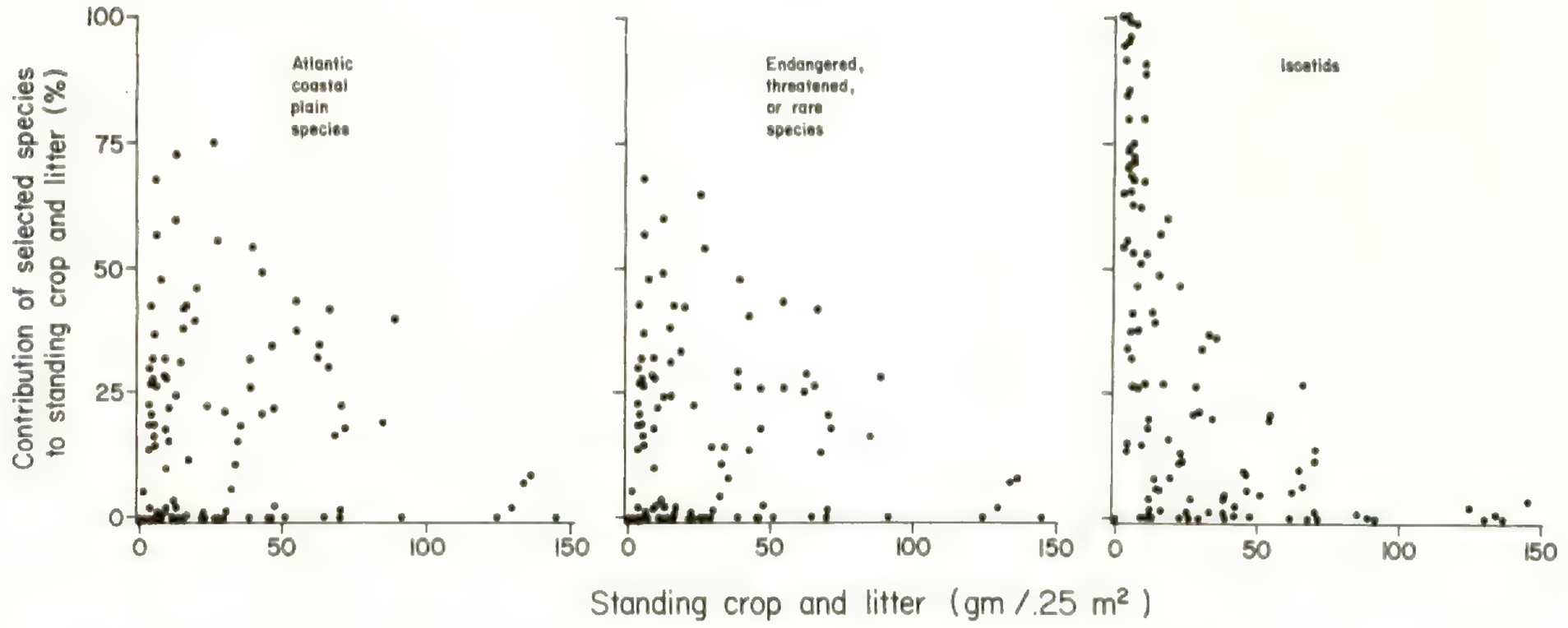



Figure 9. Contribution of selected species to standing crop and litter as plotted along a standing crop and litter gradient at Wilsons Lake, Nova Scotia (Wisheu and Keddy, 1989a). (Reproduced with permission from Elsevier Applied Science Publishers.)

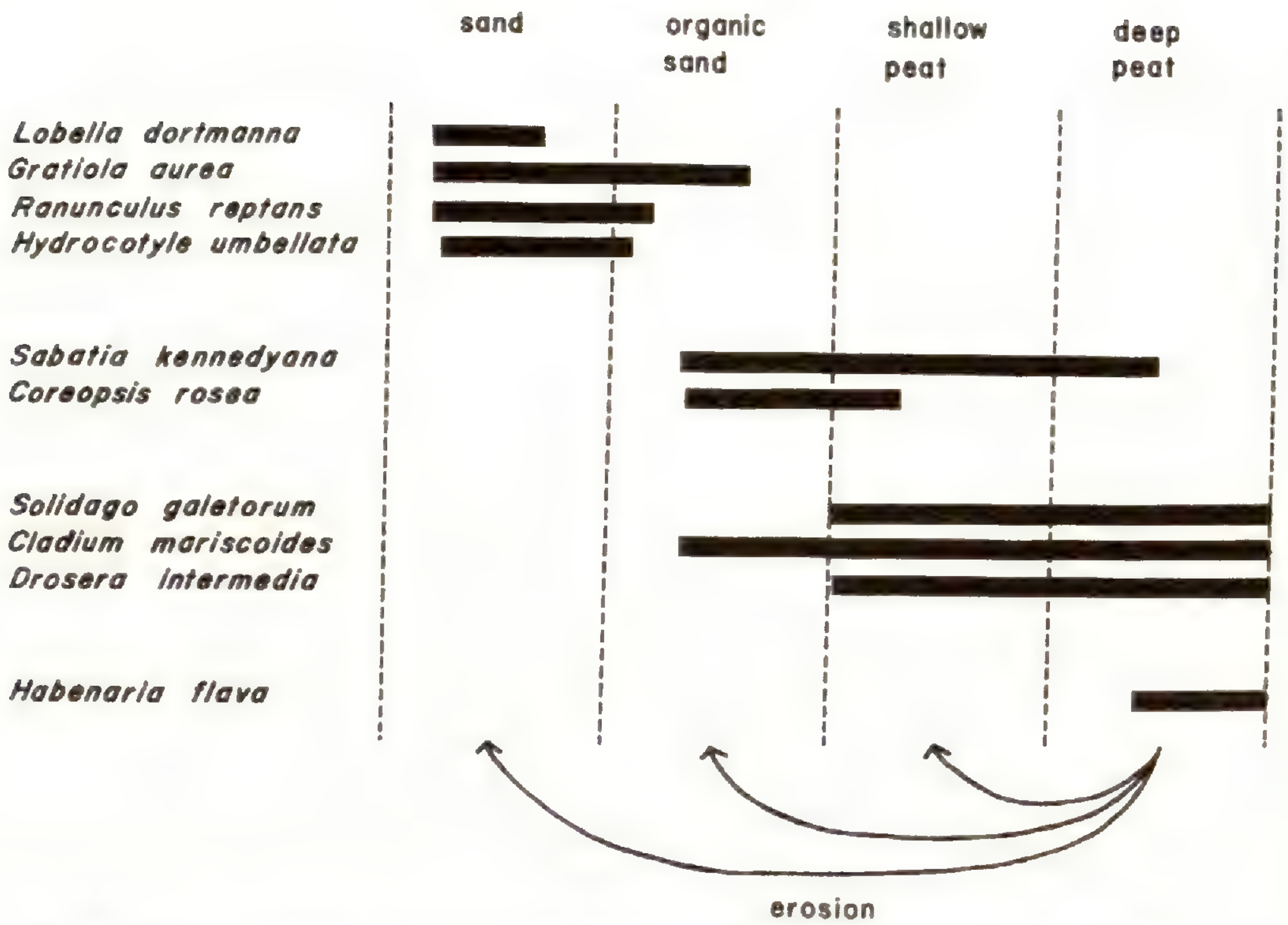



Figure 10. Apparent dynamics of vegetation on exposed shorelines. The establishment of *Cladium mariscoides* and peat accumulation are associated with increasing plant cover and changes in species composition. Erosion (arrows) reverses the process. When peat is eroded and washed up on the shoreline, it is colonized by species such as *Rhexia virginica, Panicum longifolium, Carex folliculata, Vaccinium macrocarpon, Aster nemoralis, Juncus filiformis,* and *Myrica gale.*

substrate. Where some organic material or silt is present, *Sabatia kennedyana* and *Coreopsis rosea* also occur. Once *C. mariscoides* has established and formed a shallow peat layer over the sand and gravel substrate, *Drosera intermedia, S. kennedyana, Solidago galetorum,* and *Lycopodium inundatum* increase in abundance. As peat accumulates to a depth of several centimeters, species such as *Habenaria flava* invade. Inevitably, disturbance removes the peat layer and restores the shoreline to a sand and gravel substrate. Species such as *Panicum longifolium* and *Rhexia virginica* are often found where this eroded peat has been pushed up on the shore. The exposed beaches therefore appear to have green islands of *C. mariscoides* invading gravel in some areas and being eroded away in others. A similar process appears to occur in Ontario where both *C. mariscoides* and *Rhynchospora fusca* apparently initiate succession.

## CONSERVATION

Since coastal plain species are restricted to a specific habitat within a limited geographical area, it is not surprising that many members of the flora are either endangered, threatened, or rare. Loss of habitat in both Canada and in the United States has reduced populations of some of the species to the point where the species are now threatened globally (Table 2).

If existing populations of coastal plain species are to persist, then in the long run, the stresses and disturbances that are maintaining the populations must be maintained. Stabilizing water levels, for example, would encourage shrub growth which could eliminate the coastal plain species (Keddy and Reznicek, 1982). Constant water levels would also eliminate the regeneration of the species from the seed bank (Keddy and Reznicek, 1982, 1986; McCarthy, 1987). Nutrient enrichment of the infertile shores through logging or agricultural runoff would also adversely affect the flora by encouraging the development of common, more competitive species. Such a change has already occurred in the New Jersey Pine Barrens where development has enriched sections of the barrens, sections that now have fewer rare species than pristine regions (Ehrenfeld, 1983; Morgan and Philipp, 1986).

While habitat management must be an essential part of a long term conservation strategy for these species, the greatest present threat to the coastal plain flora is simply the destruction of suitable habitat. Populations of coastal plain species on several lakes in the Tusket River system were destroyed when the lakes were turned into reservoirs by a hydroelectric dam (Keddy, 1985a). Cabin development and the associated landscaping of lakeshores (including contouring by bulldozers) have also destroyed large tracts of shoreline both in Nova Scotia (Keddy, 1985a) and in Cape Cod (B. Sorrie, pers. comm.).

All-terrain vehicles, however, are the most immediate threat to the flora. The gently sloping gravel shorelines which support the flora are ideal areas for driving the vehicles. The frequent passage of all-terrain vehicles has already destroyed 90% of what was once one of Canada's largest stands of *Sabatia kennedyana* (Wisheu and Keddy, 1989a). Damage by all-terrain vehicles may destroy not only the established vegetation, but the seed bank as well. The soil of a heavily damaged site had only 550 viable seeds/$m^2$ as compared to an intact shoreline with 10,000 viable seeds/$m^2$ (Keddy et al., 1989; Wisheu and Keddy, unpubl.).

Table 2. The Canadian, American, and global status of selected Atlantic coastal plain species.[1]

| Species | Status | | | |
|---|---|---|---|---|
| | | | U.S.A. (no. of states) | |
| | Global | Canada | Extant | Extirp. |
| *Bartonia virginica* | 5 | * | 29 (5) | |
| *Clethra alnifolia* | 5 | ** | 21 (1) | |
| *Coreopsis rosea* | 3 | *** | 7 (4) | 3 |
| *Glyceria obtusa* | 5 | | 13 (1) | |
| *Habenaria flava* | 4? | * | 17 (6) | |
| *Hydrocotyle umbellata* | 5 | *** | 26 (2) | |
| *Ilex glabra* | 5 | | 17 (2) | 1 |
| *Lacnanthes tinctoria* | 4 | * | 16 (6) | |
| *Lophiola americana* | 3–4 | ** | 9 | |
| *Lycopodium inundatum bigelovii* | 5 | | 25 (6) | 1 |
| *Panicum dichotomiflorum* | 5 | | 45 | |
| *Panicum longifolium* | ? | * | 19 (3) | 3 |
| *Panicum spretum* | ? | | 25 (1) | 1 |
| *Polygonum hydropiperoides* | 5 | | 47 (2) | |
| *Rhexia virginica* | 5 | * | 32 (4) | |
| *Rhynchospora capitellata* | 5 | | 34 | |
| *Sabatia kennedyana* | 3 | ** | 4 (4) | |
| *Sisyrinchium atlanticum* | 5 | | 27 (5) | 1 |
| *Smilax rotundifolia* | 5 | | 30 | |
| *Solidago elliottii ascendens* | 3? | | 7 (5) | 1 |
| *Solidago galetorum* | ? | * | | |
| *Utricularia radiata* | 4 | * | 21 (4) | 1 |
| *Utricularia resupinata* | 4? | | 15 (6) | 2 |
| *Utricularia subulata* | 5 | * | 19 (5) | |
| *Woodwardia areolata* | 5 | * | 27 (5) | 2 |
| *Xyris difformis difformis* | 5? | * | 23 (3) | 1 |

[1] Canadian status is from Argus and Pryer (unpubl., * rare) and the Committee on the Status of Endangered Wildlife in Canada (** threatened, *** endangered). American and global rankings are from Kartesz (unpubl.) and The Nature Conservancy (1987, scale from 5 (demonstrably secure) to 1 (critically imperiled)). The figure in parentheses is the number of states which have assigned the species a rank of 3 or less. Nomenclature follows Roland and Smith (1969) except for *Xyris difformis* Chapman var. *difformis*. Coastal plain species are those listed by Roland and Smith (1969) with the addition of *Rhexia virginica* and *Utricularia resupinata*.

There are four reasons why coastal plain species may be particularly sensitive to disturbance from all-terrain vehicles. Firstly, some coastal plain species such as *Sabatia kennedyana* are evergreen, and the loss of leaf tissue from evergreen plants not only

reduces the plants' ability to photosynthesize, but may also seriously reduce the nutrient capital of these plants which are growing in impoverished soil. Secondly, rates of recovery after a disturbance (as measured by biomass accumulation) appear to be lower along exposed shores than along sheltered shores (Sharp and Keddy, 1985). Long recovery times in such habitats would mean that relatively infrequent disturbance from all-terrain vehicles could have major impacts upon the vegetation. Third, the evidence from growth form suggests that in addition to slow growth imposed by the habitat, these species may have inherently slow growth rates, further reducing their recovery rates after disturbance. Lastly, common ruderal species such as *Juncus* spp. are most abundant in the seed bank (Figure 11; Keddy et al., 1989; Wisheu and Keddy, unpubl.). The creation of gaps within a coastal plain community would therefore allow common genera to gradually replace the rare flora if disturbance from all-terrain vehicles continues.

Threats to the coastal plain flora are both numerous and widespread so it is imperative that we act quickly to preserve what remains. Disjunct populations are at particular risk because once extirpated, there are no immediately adjacent plants that can recolonize (Reznicek, 1989). Also, protecting whole habitats as a general conservation strategy increases the probability that the protected system will be self-perpetuating and more resistant to the occasional perturbation. This same strategy also maximizes efficiency by allowing many species to be protected at once. The establishment of Nova Scotia's first nature reserve in the Tusket River system protected not one, but eight significant species. Careful selection of future reserves can further multiply the number of species that are secure in at least one region.

Local priorities, however, must not be the only criteria with which to select new reserves and new target species. One must consider status in other regions. *Clethra alnifolia,* for example, has the same Canadian rank (threatened) as *Sabatia kennedyana*; yet *C. alnifolia* is common in the United States (Table 2) while *S. kennedyana* occurs in only four states, all four of which consider it rare. An ecological reserve, then, to protect *C. alnifolia* would be a lower global priority than a reserve to protect a population of *S. kennedyana.* There is a clear need to look beyond provincial or national boundaries when establishing conservation priorities.

The long term maintenance of the landscape and watershed

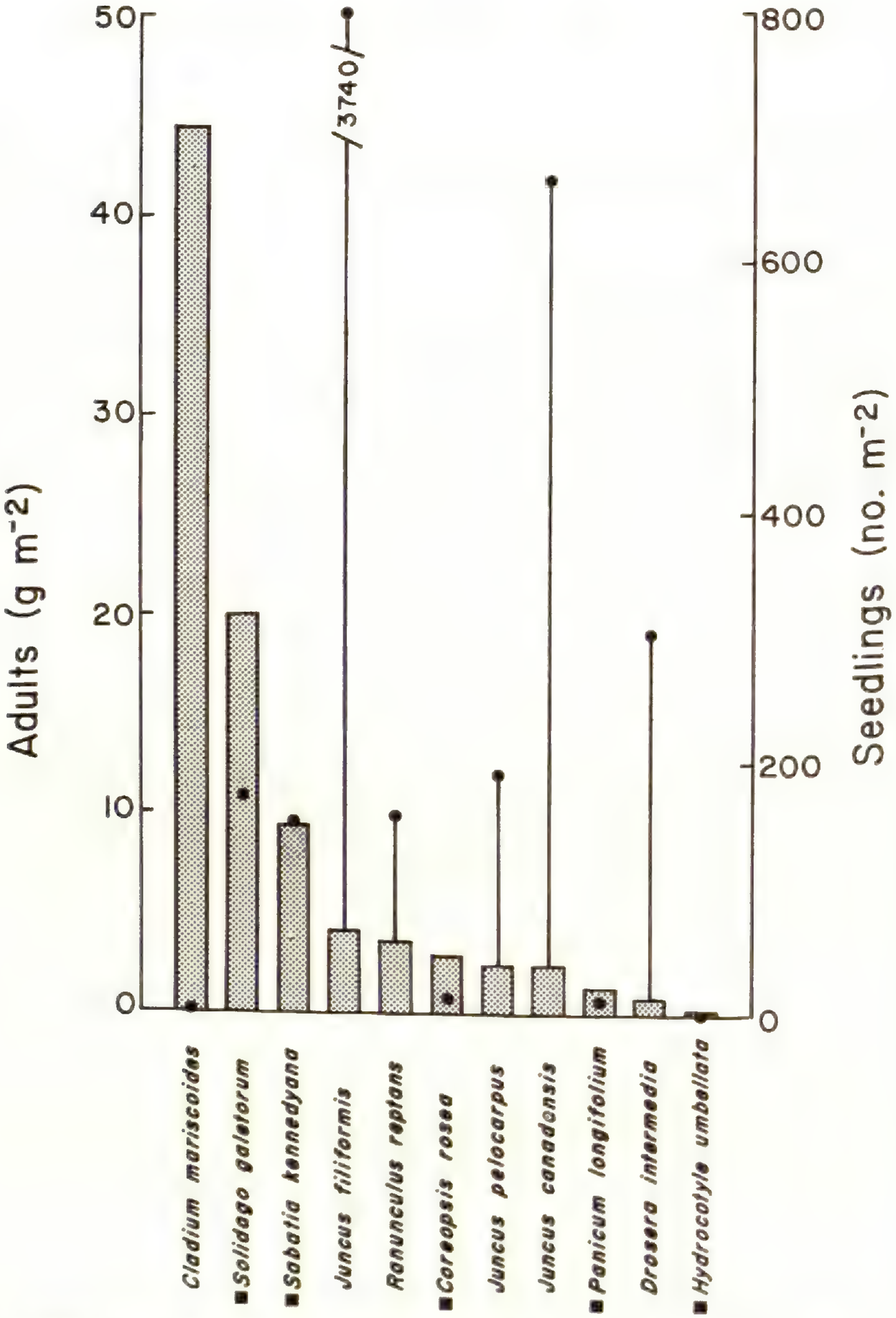



Figure 11. Occurrences of selected species as adults and as germinable seeds in the seed bank at Wilsons Lake, Nova Scotia. Coastal plain species are indicated with solid squares (Keddy et al., 1989). (Reproduced with permission from Academic Press, Inc.)

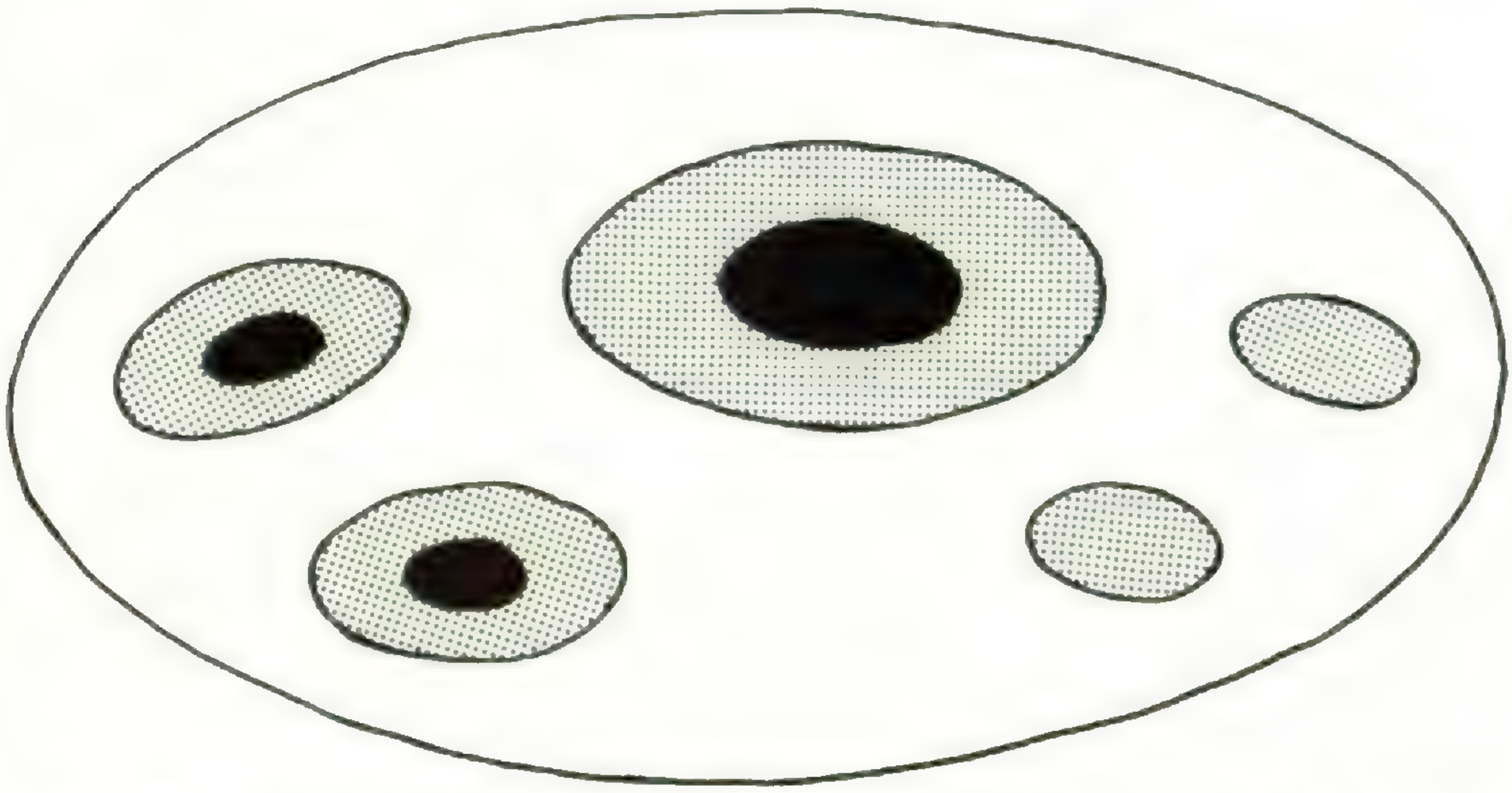


Figure 12. An integrated reserve system: reserves are shown in black, buffer zones are stippled, and the management area with educated and concerned landowners is white. The scale of the diagram can vary from a watershed to an entire state.

around reserves is also essential. The selection of target species and the establishment of new reserves should be followed by a public relations campaign aimed at educating local landowners. Brochures and exhibitions could modify land use activities that are detrimental to the reserve and its flora. People could be taught, for example, to keep all-terrain vehicles off lakeshores. An educated public would also facilitate the establishment of buffer zones around reserves. Fewer people would oppose the zones while educated landowners would be more willing to act as land stewards. Finally, an educated public could minimize the need for more reserves. The Nova Scotia museum is now actively involved in such a program.

The long term goal, then, of plant conservation should be a reserve system that integrates reserves into the surrounding landscape (Figure 12; *see* Katz, 1986, for example). Buffer zones around reserves that are surrounded by educated, concerned residents will not only protect the target species but will also preserve a variety of other vegetation types. The ultimate objective of such a system should not only be to keep a list of species present, but to represent the range of vegetation types and array of natural communities in which they occur.

In conclusion, our knowledge of biogeography and ecology of coastal plain species has increased significantly over the past de-

cades. But this knowledge must be used to guide a more aggressive, long term conservation strategy for coastal plain plants in North America as a whole. Points to consider when designing such a strategy include 1) preserving whole habitats, 2) considering the global status of species, and 3) establishing conservation plans that incorporate reserves, buffer zones, and community education and participation.

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# PROGRESS IN RARE PLANT CONSERVATION IN MAINE

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## ABSTRACT

The last decade has brought significant advances in knowledge and conservation of rare plant species in Maine. The status of rare species in the state is reflected in the Official List of Maine's Plants that are Endangered or Threatened, recently compiled by the Maine State Planning Office. Systematic inventories by the Maine Critical Areas Program and The Nature Conservancy's Natural Heritage Program have uncovered numerous new populations of species of national concern, and stations for over 50 species for which there were no known extant stations eight years ago. However, 91 species are still considered possibly extirpated in Maine. While 34% of these are northern species, 57% are southern species reaching the northern limits of their ranges in southwestern Maine. It is not known whether this disproportion reflects uneven inventory effort or a greater number of local extinctions.

In the last eight years, private conservation organizations have acquired ten sites totalling 2000 acres to protect 45 species of plants. The voluntary cooperation of numerous state agencies, as well as over 225 private landowners, has been enlisted in protecting 168 rare plant stations placed on the Register of Critical Areas. Maine still lacks legislation specifically protecting rare plants. Thus, the principal hopes for further progress in rare plant conservation in Maine lie in continued public education, landowner cooperation, and especially acquisition of critical habitat.

Key Words: Maine, endangered, conservation, rare plants

The last decade has brought significant advances in our knowledge of rare plant species in Maine and important strides in their conservation. The current understanding of the status of rare species in the state is reflected in the Official List of Maine's Plants that are Endangered or Threatened which was recently compiled by the Maine State Planning Office (Dibble et al., in prep.). This list includes 84 Endangered and 74 Threatened taxa. While this list is a direct descendant of previous efforts, including that of the NEBC (Eastman, 1978), it is important as the first result of 1986 state legislation authorizing the creation and maintenance of an official list of rare plant species and thus represents a notable advance in public and governmental awareness of rare plant conservation needs.

Effective endangered species conservation depends on three basic components: identification, education, and protection. The obvious and essential first step is knowing what you have—what species are rare and where they occur. The initiation of a Natural Heritage Program by the Maine Chapter of The Nature Conservancy, increased state funding for the addition of a botanist to the staff of Maine's Critical Areas Program, and the signing of a Limited Cooperative Agreement between the State Planning Office and the USF&WS Office of Endangered Species have contributed to a substantial increase in the resources devoted to the inventory of rare plants in the state.

Recent inventory effort has focused on several centers of plant rarity in Maine: coastal Washington and Hancock Counties (Olday et al., 1983), St. John and Aroostook Rivers (Gawler, 1983), estuaries of the Kennebec and Penobscot Rivers, northern peatlands, especially ribbed fens and other circum-neutral wetland habitats (Davis et al., 1983; Sorenson, 1986; Widoff, 1988) and alpine areas of Mt. Katahdin (Hudson, 1985) and the Mahoosucs (Burke, 1982; Hudson, 1986). Inventories in York and Cumberland Counties have targeted likely habitat for selected species such as *Isotria medeoloides, Carex polymorpha,* and *Iris prismatica.*

While current state lists (Dibble et al., in prep.) include almost all the species on previous lists by Eastman (1978) and Gawler (Critical Areas Program, 1981), new knowledge of their distribution and abundance has changed the recognized status of many species. Happily, the news is mostly good; often (with some notable exceptions), the more we look the more we find. Inventories sponsored by the Maine Critical Areas Program and the Natural Heritage Program, in cooperation with the USF&WS, have uncovered new populations for species of national concern such as *Isotria medeoloides, Pedicularis furbishiae, Carex polymorpha, Carex oronensis, Cardamine longii,* and *Eriocaulon parkeri* (Table 1). At least six species not previously known to occur in the state have been discovered in the past decade: *Minuartia rubella, Dentaria laciniata, Drosera anglica, Carya cordiformis, Sporobolus asper,* and *Polemonium vanbruntiae.* Stations have been established for over 50 species for which there were no known stations eight years ago. Many additional stations have been located by volunteers. As many as 36 species formerly considered rare or even threatened have now been placed on a general watch list (Vickery et al., 1985).

Table 1. Current status in Maine of taxa listed, proposed, or under review as Threatened or Endangered by the U.S. Fish and Wildlife Service.

| Species | Status in 1980[a] | Status in 1985[b] | No. of Known Sta. 1981[c] | No. of Known Sta. 1987[d] |
|---|---|---|---|---|
| *Pedicularis furbishiae* | Listed End. | Listed End. | 8 | 11 |
| *Isotria medeoloides* | Prop. End. | Listed End. | 2 | 12 |
| *Paronychia argyrocoma* v. *albimontana* | Prop. End. | Withdrawn | 2 | 5 |
| *Carex oronensis* | Under review | Under review | 1 | 23 |
| *Scirpus longii* | Under review | Under review | 0 | 0 |
| *Listera auriculata* | Under review | Under review | 1 | 7 |
| *Plantanthera leucophaea* | Under review | Prop. Threat. | 1 | 1 |
| *Cardamine longii* | Under review | Under review | 2 | 8 |
| *Oxytropis campestris* v. *johannensis* | Under review | Under review | 4 | 8 |
| *Viola novae-angliae* | Under review | Under review | 0 | 9 |
| *Mimulus ringens* v. *colpophilus* | Under review | Under review | 0 | 4 |
| *Valeriana sitchensis* ssp. *uliginosa* | Under review | Withdrawn | 3 | 9 |
| *Prenanthes boottii* | Under review | Under review | 2 | 3 |
| *Eriocaulon parkeri* | — | Under review | 3 | 21 |
| *Carex polymorpha* | — | Under review | 0 | 3 |

[a] U.S. Fish and Wildlife Service, 1980.
[b] U.S. Fish and Wildlife Service, 1985.
[c] Critical Areas Program, 1981.
[d] Dibble et al., in prep.

By comparison, documented losses of rare species in recent years have been apparently few, although timber harvesting has destroyed critical habitat and decimated populations at several known rare plant stations. However, 91 species are still considered possibly extirpated in Maine because no stations for them have been documented in the last 20 years. Interestingly, while 34% of these possibly extirpated taxa are northern species reaching their southern range limits in Maine, 57% are southern species, typically only known from one or two herbarium records over 80 years old from York or Cumberland County. There have been re-discoveries of 21 out of 41 historic northern species as opposed to only 16 out of 62 southern plants for which there were no known extant stations in 1981 (Critical Areas Program, 1981). The high proportion of southern species not relocated may reflect

uneven inventory effort. Alternatively, this may reflect a greater number of local extinctions due to natural causes such as increasingly severe winters, or habitat destruction in this rapidly developing part of the state.

Many more rare plant stations are destroyed through ignorance than intention. The second key step in conservation is education—getting the information to the public, the landowners, and land managers. Maine's Critical Areas Program has contributed by publishing and disseminating planning reports and botanical fact sheets on 146 species, an educational brochure on *Pedicularis furbishiae,* an addendum to *Rare Vascular Plants of Maine,* and a compilation of distribution maps for all rare plant species. The Program has cosponsored two statewide endangered species conferences to encourage public awareness and participation in rare plant conservation. Since 1974, the Critical Areas Program has placed 168 botanical sites on the Register of Critical Areas, Maine's official list of special areas worthy of conservation. A key component of the program is notification of landowners of rare species on their land, providing them with information on the species' biology and habitat needs, and soliciting their voluntary cooperation in the protection of the plants. To date, over 225 landowners of rare plant sites have been contacted. The booklet *The Landowner's Options* (Milne, 1985), explaining the variety of land conservation strategies available in Maine, is provided to each landowner. The 85% response rate to the biennial status update mail survey is one indication of the success of this landowner notification effort.

The third and most critical component of conservation is actual protection of the rare species and their habitats. One potential tool for providing such protection is through legislation. Maine still lacks legislation specifically protecting rare plant species from exploitation or habitat destruction. The Natural Resources Protection Act provides incidental protection to some Endangered and Threatened plants by regulating activities in coastal wetlands, inland freshwater wetlands, Great Ponds, streams, and areas above 2700 feet in altitude. However, freshwater wetlands smaller than ten acres are not included and activities such as peat mining, normal forestry, and agriculture are exempted from review. State guidelines included in the Mandatory Shoreland Zoning Act name endangered plants as one of the natural resources for towns to consider in establishing Resource Protection Zones. However,

municipal officials responsible for issuing permits or variances are not systematically informed of the presence or location of such species in their jurisdiction. Other laws such as the Site Location of Development Act require protection of "unique resources," but there are not clearly defined and do not explicitly refer to endangered plant species.

The 1983 Maine Rivers Bill, which prohibits new dam construction and limits shoreline development on 1100 miles of rivers with outstanding values, provides some protection to the habitat for 15 Endangered and Threatened species (Maine River Study, 1982). However, key sections of the St. John and Penobscot Rivers where such species as *Pedicularis furbishiae* and *Carex oronensis* occur are not protected under this act.

In the absence of effective, comprehensive state regulation, the primary tool for rare plant protection must be habitat acquisition and management. In the last eight years, private conservation organizations have secured legal interests in 12 sites totalling over 2000 acres that provide habitat for 27 species of rare plants. The habitats included in these projects range from a northern fen at Woodland Bog, to Rocky Island in the St. John River, to a portion of a sandplain grassland at the Kennebunk Plains, to a *Chamaecyparis* stand on a domed peatland at Saco Heath. Eight preserves of The Nature Conservancy protect habitat for four Endangered species and 14 Threatened species. Five additional sites with Endangered or Threatened species are owned by the New England Wildflower Society and local land trusts.

State and federal agencies own a number of rare plant sites in Maine, most notably Mt. Katahdin and associated areas in Baxter State Park where there are 45 Endangered, Threatened, and Special Concern plant species. Land management plans recently developed by the Bureau of Public Lands for the Mahoosucs, Deboullie Lake area, and Allagash Lot on the St. John River and the Department of Inland Fisheries and Wildlife for the Vern Walker Wildlife Management Area specifically attempt to accommodate the needs of eight Endangered and Threatened plant species. A number of Endangered and Threatened species occur on federal lands such as Acadia National Park and the Rachel Carson Petit Manan Wildlife Refuges.

Of 92 Critical Areas with Endangered or Threatened species, 11 are at least partially owned by private conservation organizations and 18 are owned entirely by state, federal, or town gov-

ernments. At least one station for 36 Endangered (42% of total in state) and 34 Threatened species (46%) is currently owned by a federal, state, or private conservation agency.

Passage in 1987 of a $35 million bond issue for acquisition of natural land greatly enhances prospects for rare plant conservation in Maine, both because it includes the presence of endangered species habitat as one of the potential criteria for site selection and because it requires that any land acquired with these funds be inventoried for rare species and managed so as to perpetuate them.

Where are the Endangered and Threatened species still in need of protection? Fortunately, two of Maine's major concentrations of rare species are already protected: the Mt. Katahdin area and Crystal Bog. However, the St. John River with Furbish's Lousewort and four other Endangered and six Threatened species is not yet secure, nor is Twin Peaks in northern Oxford County, where nine Endangered or Threatened species occur. Such sites represent especially high priorities and clear conservation challenges in the coming years.

The remaining unprotected species are not evenly scattered across the state. Perhaps not surprisingly, nearly half occur in specific limited habitats unsuitable for development in any case, such as cliffs, pond or river shores, or saltmarshes. These species could be protected if natural resource protection statutes already in place were substantially strengthened and rigorously enforced. Of the remaining upland plants of woods, fields, and roadsides—especially vulnerable to habitat destruction through logging or development—more than half occur in forested areas of the southernmost counties, which are also experiencing the most rapid development. This threat, combined with the high proportion of historic and unrelocated species in this area, suggests that York, Cumberland, and southern Oxford Counties should receive high priority for both inventory and protection activities in the immediate future.

Important progress has been made in rare plant conservation in Maine. With increased inventory effort, many sites for rare plants have been discovered or relocated; landowners of the majority of these sites in Maine have been notified. The public in general, and state and town regulatory and planning officials especially, is increasingly aware and concerned for the needs of rare species. Nearly half of the species listed as Endangered or

Threatened in Maine occur on land owned by a government or private conservation agency. The creation of an Official List of Endangered and Threatened Species has focused priorities for additional land conservation and management efforts in both the public and private sectors.

On the other hand there are many challenges remaining. There are over 90 species with fewer than five known stations in the state for which there is no protection by conservation ownership or state regulation. The additional 91 historic species for which no extant stations have been found should signal the urgency of the conservation task, as Maine is now experiencing the kind of development already long underway in southern New England. We will undoubtedly lose more species soon unless prompt action is taken. We need to continue to inventory, educate, strengthen our natural resource and endangered species laws, and, especially, bring more critical habitat under protective stewardship.

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# NOTES ON THE RARE FLORA OF NEW HAMPSHIRE

FRANKIE E. BRACKLEY AND GARRETT E. CROW

## ABSTRACT

The status of the on-going floristic survey of the rare plants of New Hampshire is discussed with particular emphasis on the situation both before and after the 1978 publication of *Rare and Endangered Vascular Plant Species in New Hampshire.* Records of the new state occurrences discovered by the New Hampshire Natural Heritage Inventory are provided. Information on the legal status of rare plant species in the state pursuant to the 1987 Plant Protection Act and the Federal Endangered Species Act is provided.

Key Words: Endangered, threatened, flora, vascular plants, New Hampshire

## INTRODUCTION

Great strides have been made in our understanding of the rare floristic elements of the state of New Hampshire. In 1973, a preliminary listing of the endangered species of vascular plants of New Hampshire was published by Dr. Albion R. Hodgdon, Professor of Botany at the University of New Hampshire. After "Doc" Hodgdon was incapacitated by injuries suffered in a tragic accident, Dr. Garrett E. Crow assumed Hodgdon's duties at the University. Crow and his graduate student, Irene M. Storks continued work on the endangered species project. During the summers of 1977 and 1978, Storks conducted field work resulting in important documentation and re-verification of a number of rare plant occurrences. Field work was concentrated in the White Mountain National Forest, and a report of the results was prepared for the U.S. Forest Service (Storks and Crow, 1979).

In addition, Storks and Crow were the New Hampshire representatives on the Endangered Species Committee of the New England Botanical Club, which had as its goal the publication of lists of rare, threatened, and endangered species of each New England state. In 1978, *Rare and Endangered Vascular Plant Species in New Hampshire,* an annotated list, was published (Storks and Crow, 1978). The following year the New England Botanical Club hosted a symposium on "Rare and Endangered Vascular Plant Species in New England" resulting in the publication in *Rhodora* (Vol. 82, No. 829) of the series of papers presented at

the symposium. Crow and Storks (1980) contributed a paper entitled "Rare and Endangered Plants of New Hampshire: A Phytogeographic Viewpoint." These two works are extremely valuable compilations of the information available prior to 1979 on the rare and/or declining flora of New Hampshire.

During the 10 years that have elapsed between the publication of the 1978 book and the present, there has been increased activity in the area of rare plant investigation. During the years of 1979–81, while doing field work for a master's thesis on the orchids of New Hampshire, Frankie Brackley discovered many new sites for species considered rare in the state and reverified several historic records (Brackley, 1981, 1985).

In 1982, the New England Natural Heritage Program was initiated by The Nature Conservancy. Its function was to collect and analyze data on rare fauna, flora, and natural communities primarily in the states of New Hampshire and Vermont. Frankie Brackley and Thomas Rawinski were hired as the Botanist and Plant Ecologist, respectively, for the program. The Heritage Program effort began by searching additional herbaria and compiling more information on the historic distribution of rare plants in New Hampshire. Subsequent field work by Brackley, Rawinski, and contract botanist John Korpi continued to uncover many new sites for rare plants in the state. In a few cases, enough new sites were discovered to justify deletion of a species from the "rare" list.

During the summer of 1982, Debra Dunlop and Garrett Crow worked under a coastal zone grant on an inventory of rare plants occurring in the coastal region of New Hampshire (Dunlop and Crow, 1985a, 1985b). This work updated many of the known records of rare plant occurrences, added new sites and increased our understanding of the flora of this area. For the next two years, The Nature Conservancy contracted Dr. Clotilde Straus to conduct field work in the seacoast region, focusing primarily on estuarine sites. Dr. Straus, who has botanized this area of New Hampshire for many years, was able to document many additional records for rare plants.

In 1984, The Nature Conservancy, in cooperation with state and private conservation agencies began operation of the New Hampshire Natural Heritage Inventory in Concord, New Hampshire, with Brackley and Korpi as part of the Heritage staff. In 1986, the Heritage Program was incorporated into state govern-

ment within the Department of Resources and Economic Development (DRED). The program presently inventories for 379 plant species considered endangered, threatened, or rare in the state. Occurrences of these species are mapped and the data are computerized employing standardized methodology developed by The Nature Conservancy and utilized by the 47 existing state heritage programs.

This paper will provide some of the notable additions to the 1978 rare plant publication and will discuss recent efforts for rare plant conservation. Storks and Crow (1978) listed 404 species of rare and endangered vascular plant species of New Hampshire. The present Heritage Inventory list excludes approximately 40 of these species, which have been found to be more common than previously known, are of questionable taxonomic status, of non-native origin, or whose records were based on misidentified specimens. A complete revision of the rare vascular plant list is under preparation by Brackley and Crow.

## NEW STATE RECORDS (NATIVE SPECIES ONLY)

*Valeriana uliginosa* (T. & G.) Rydb. was discovered by Brackley in 1980 growing in a northern white cedar swamp with *Cypripedium reginae* Walt., *C. parviflorum* Salis., and other calciphiles (*Brackley 4576*, NHA).

*Carex eburnea* Boott was found on the face of Holt's Ledge in Lyme, Grafton County by Rawinski and Brackley on 20 October 1983 (*Rawinski & Brackley 927*, NEBC). Several other species rare for the state, including *Juniperus horizontalis* Moench and *Aster ptarmicoides* (Nees) T. & G., occur at this site.

*Uvularia perfoliata* L. had been mentioned in the literature as occurring in Plainfield, however the specimens from that town in the Jessup Herbarium at Dartmouth (J. Poole, pers. comm.) and Hodgdon Herbarium at UNH have been determined to be *U. grandiflora* Sm. Yet on June 1, 1984, Brackley and Korpi discovered *U. perfoliata* L. growing in Hinsdale, Cheshire County (*Brackley & Korpi 6711*, NHA). The following year, Rawinski found a second population of this species growing in Windham, Rockingham County (*Rawinski 2837*, NEBC).

*Eriophorum angustifolium* Honckeny was found at Heath Pond Bog in Ossipee, Carroll County by Rawinski, Brackley, and Jan Cassin on June 6, 1984 (*Rawinski, Brackley & Cassin 1186,* NEBC). Though extremely abundant in a vegetative condition, fertile culm formation may be variable from year to year.

*Arisaema dracontium* (L.) Schott had been reported (Beetle, 1938) as occurring in Fox State Forest in Hillsboro, New Hampshire, and indeed there is a collection of this species in the Fox Forest herbarium. But because there appears to be no appropriate habitat for the species in this state forest, it is possible that this specimen was mislabeled as to location. In our region, the species is typically found in floodplain forests. It was in such a habitat where the first authentic record for New Hampshire was found by Rawinski, Cassin, and Libby Hyde in 1984 (*Rawinski, Cassin & Hyde 1357,* NEBC). Two years later Brackley and Elizabeth Thompson, the botanist for the Vermont Natural Heritage Program, discovered a second site for the Green Dragon, also in a floodplain forest (*Brackley & Thompson 86-80,* NHA). Both sites are along the Connecticut River.

*Betula pumila* L. is a boreal species of fens and swamps, often in calcareous sites. John Korpi discovered a large colony of this species growing in an uncharacteristic acidic habitat on state property in Ossipee in 1985 (*Korpi 3499,* NHA).

*Cyperus erythrohizos* Muhl. was collected in New Hampshire for the first time by Garrett Crow, Anne Stancioff, and Tom Mione in 1985 in Strafford County (*Crow, Stancioff & Mione s.n.,* NHA, NEBC).

## VERIFICATION OF SELECTED HISTORIC RECORDS

*Cypripedium reginae* Walt. was listed by Storks and Crow (1978) as possibly extinct for New Hampshire since it had not been seen in the state since 1891. In 1979, Brackley, acting on information supplied by Fred Steele, found two populations of Showy Lady's-slippers (Brackley, 1979) and another locality in 1980 (*Brackley 4210,* NHA). Additional sites were discovered in 1982 and 1983 by Rawinski and Caren Caljouw and by Rawinski and Brackley, respectively, bringing the number of known stations for this spectacular Lady's-slipper to five.

*Isotria verticillata* (Muhl. ex Willd.) Raf. had been last documented from New Hampshire in 1909. In 1983, John Korpi discovered a population of this orchid growing in Cheshire County (*Korpi 916*, NHA). At present, it is the only extant station known for this species.

*Corallorhiza odontorhiza* (Willd.) Nutt. was not known to be a part of our flora until a specimen was found in the University of Vermont herbarium from "Hart's Island, Vermont" (Marc DesMueles, pers. comm.). While one can drive onto Hart's Island from the Vermont side of the Connecticut River at low water, the island is technically in the state of New Hampshire. A Natural Heritage field survey to that site failed to turn up the species. However, in 1984 Brackley and Rawinski found a small population in the eastern part of the state, in Carroll County (*Brackley & Rawinski 7416*, NHA), and Brackley and Korpi discovered another occurrence in the same county the following year. Both populations were growing in areas that support several other orchid species.

*Cardamine bulbosa* (Schreb.) BSP. had been last collected in the state in 1915 in Rockingham County. Early in May of 1986, Brackley rediscovered this species growing in a seepage swamp (*Brackley 86-30*, NHA) that also supported scattered trees of Atlantic White Cedar.

*Viburnum rafinesquianum* Schultes, a species occurring at the northeastern edge of its range, was rediscovered by John Korpi in 1986 (*Korpi 86-393*, NHA). This shrub occurs as an understory dominant in a dry oak-hickory forest in Rockingham County. It had been last documented in New Hampshire in 1916.

*Cypripedium arietinum* R. Br., the Ram's Head Lady's-slipper, has apparently declined in numbers in New Hampshire. In 1983, Brackley relocated a remnant of a historic population in Belknap County. In 1985, Bruce Sorrie, of the Massachusetts Heritage Program, relocated a separate population occurring in the same town. No new localities of this species have been found since 1936.

*Isotria medeoloides* (Pursh) Raf. was documented by six historic occurrences in the state of New Hampshire, but no extant sites were known to the academic community at the time of the NEBC

rare plant symposium in 1979. Brackley turned up three new sites for the orchid during her thesis research. In 1984, Rawinski and Brackley began to identify potential habitats for the orchid using soils maps, and many populations were discovered. Of the 17 populations of Small Whorled Pogonia found since 1984, four have been destroyed by development, logging, or theft (Rawinski, 1986).

## LEGAL STATUS AND CONSERVATION OF RARE PLANTS IN NEW HAMPSHIRE

Three vascular plants occurring in New Hampshire are listed as "endangered" under the federal Endangered Species Act of 1973, as amended. They are *Isotria medeoloides* (Pursh) Raf. (Small Whorled Pogonia), *Potentilla robbinsiana* Oakes (Robbins' Cinquefoil), and *Astragalus robbinisii* var. *jesupi* Egglest. & Sheldon (Jesup's Milk-vetch). Of the three, only *Potentilla robbinisiana* Oakes is located on federal land (within the White Mountain National Forest) and is therefore afforded the full protection of the Endangered Species Act.

On May 18, 1987, the New Hampshire legislature passed "The New Hampshire Native Plant Protection Act of 1987." One provision of this act mandates the Department of Resources and Economic Development (DRED) to produce lists of those species determined to be Endangered, Threatened, or of Special Concern in the state. This process has been carried out with the advice of the New Hampshire Natural Areas Council and the best scientific information available. On April 16, 1988, a public hearing/rare plant conference was held to present the draft lists and solicit input from the public. At present, the draft lists of protected plants consist of 139 species considered Endangered, 144 species considered Threatened, and 11 species of Special Concern.

The Act provides a mandate for DRED to establish conservation programs for the protection of listed species and allows it to enter into agreements with other agencies and private organizations to fulfill this aim. DRED may also acquire property in order to protect listed plants. In addition, other state agencies must consult with the department to ensure that none of their actions will jeopardize the continued existence of any protected plant species.

It is hoped that, with ongoing botanical investigations in New Hampshire, a better understanding of the status of our rare plant

species in the state is emerging. With the passage of plant conservation legislation and ensuing public awareness of the existence and value of our rare native plants, state and private conservation organizations have the necessary information, as well as a mandate, to protect ecologically significant habitat. For, as Hodgdon (1973) pointed out, "By far the more effective course of action is to set aside the areas where the rarest plants and other endangered species grow."

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# RARE PLANT CONSERVATION IN VERMONT IN THE 1980'S

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The value of rare species has increased dramatically in the public mind in the last two decades, a result of the increased appreciation of the fragility and vulnerability of all our natural resources. In Vermont, a state with a long history of environmental awareness, this appreciation has had an especially profound effect. This paper will review the history of rare plant protection in Vermont, and summarize the important advances of the 1980's.

The early botanical explorers in this state were avid plant collectors; they apparently saw it as their duty (for some it was a livelihood) to provide herbaria with an adequate supply of collections of each species, particularly the unusual ones. Little concern was expressed about the potential for such collecting to result in decline and decrease in native plant populations. Neither, it seems, was there any concern about the loss of native plants to development. Countryman (1980) cited the example of *Astragalus robbinsii* Oakes, a Vermont endemic discovered on the Winooski River in 1829 and extinct by 1894. A dam was constructed that flooded the only colony of the species, but its doom may have been sealed earlier by overcollection. Cyrus Pringle (1897) remarked that from the station, there ". . . had been gathered a supply of these plants sufficient for all the herbaria of the world."

*Listera australis* Lindl., extant but quite rare in Vermont, is a plant of the southern United States with local outlier populations north to Quebec. Two populations were known historically from Vermont, but only one is extant. H. W. Child (1922) described an expedition to a Vermont bog to find the plant: "In a short time [Mr. Horsford] came to me with a plant of *Listera australis*. . . . We then hunted for more and found four. . . . All were then carefully packed and taken to Boston." He then listed the herbaria to which the specimens were distributed, described Horsford's pride at having found the plants, and explained that the location of the station should be kept a secret. Dutton (1927) described another expedition in search of the plant, again to a secret location (perhaps the same one), and proudly stated: "Several specimens were collected so that *Listera* might be represented

in each of the leading herbaria of the state." In spite of the zealous collectors of the 1920's, at least one population of the species (albeit a small one) remains.

Other plants have not fared as well. Our current list of missing species (once reported from Vermont but not seen in the last 25 years) numbers more than 70 (Jerry Jenkins and Vermont Natural Heritage Program, unpubl. data). The Natural Heritage Program has made the search for missing species a priority, but many remain missing, either because they are difficult to locate, or because they have been lost to thoughtless overcollection or development. For a very few of these plants, climatic change may be responsible for their loss.

The first plant protection law in Vermont was passed in 1921. This law (37 P.L. 8578) protected certain plants from picking; it was apparently a response to the threats imposed by collection of plants for the florist trade. The plants protected were not necessarily the rarest in the flora, but were showy and desirable plants that might have been vulnerable to such use. All orchids were on the list, for example, including the now common, almost weedy alien *Epipactis helleborine* (L.) Krantz. In 1957 a new Endangered Species statute was enacted by the Vermont Legislature (13 V.S.A. 3614), through which a few species were added to the list. The law was replaced in 1972 by a new statute (13 V.S.A. 3651-3), but no amendment was made to the list.

Unfortunately, little attention was paid to the actual list of threatened and endangered species in Vermont, and in the early part of this decade it stood almost as originally constituted, by then badly out of date. It was outdated in three senses: 1) in the 60 years since the passing of the first law and compilation of the list, much new information had been gathered about the rarity and distribution of the plants on the list, as well as others, 2) the status of a few species on the list (such as *Epipactis*) had changed dramatically, and 3) the primary threat to native wild plants had become development rather than collecting.

With the environmental movement of the 1970's came a number of significant advances in the awareness and protection of native wild plants. The Federal Endangered Species Act (P.L. 93-205) was passed in 1972, providing for protection of plants and animals in danger of extinction throughout their natural ranges. In 1974, The Nature Conservancy established its first state Natural Heritage Program (in South Carolina) to inventory and mon-

itor rare plants, animals, and natural communities at the state level. Of more local significance, the U.S. Fish and Wildlife Service in the early 1970's initiated the publication of a report on rare plants for each of the New England states. For Vermont, this resulted in the first useful, up-to-date state list of rare and endangered plant species (Countryman, 1978).

These activities have spurred further awareness and activity in rare plant protection. The 1980's have seen significant changes in rare plant protection in the state. In this decade: 1) the Vermont Natural Heritage Program was established, 2) there has been a consequent dramatic increase in rare plant protection activities on the part of The Nature Conservancy and other private conservation groups, 3) state government has incorporated data on rare plants into its state lands management plans and environmental review processes, 4) the Vermont Botanical and Bird Clubs have published a bulletin after a hiatus of 30 years, and 5) the Vermont Endangered Species Law has seen significant amendments and updates.

The Vermont Natural Heritage Program was established in 1983, first within the New England Natural Heritage Program at the Nature Conservancy's Eastern Regional Office. The fledgling program compiled historical data and prepared lists of rare species and natural communities for Vermont and provided for an inventory of rare plants in the state. In 1984 the program moved to the Vermont Field Office of The Nature Conservancy, and in 1987 was transferred to state government. It is now operated as a unit of the Vermont Agency of Natural Resources, and as such is able to interact easily and efficiently with state regulatory and land management agencies.

Each year since the program's inception in 1983, significant advances have been seen in our understanding of the status of rare plants in the state. In 1985, for example, the program conducted an inventory of rare plants on the Lake Champlain Islands, re-locating several so-called missing species. The inventory was inspired by the re-location in 1984 of *Lathyrus ochroleucus* Hk. (it had last been collected in the state in 1910). This is one of a handful of plants that are more common westward and reach their eastern limits in the Champlain Valley of Vermont. It was found on an uninhabited island in a woodland sedge opening, a habitat that is mostly restricted in Vermont to the Champlain Islands but may mimic habitats found in the prairie states. The

1985 inventory yielded new information on other missing species as well as other range limit species. Of particular interest are *Astragalus canadensis* L., with only seven extant stations in Vermont, *Lathyrus japonicus* Willd., a relict of the marine invasion of the Champlain basin, with only five sites known, and *Paronychia canadensis* (L.) Wood, known only from a Lake Champlain Island and the Pownal Hills in extreme southwestern Vermont. In all, about 75 new rare plant stations were found in the inventory.

This new knowledge gave impetus to The Nature Conservancy and other conservation groups to increase their protection efforts for rare plants. In 1986, for example, The Nature Conservancy contacted over 30 landowners of rare plant sites, including several islands, and arranged for voluntary protection of those sites. Included was our only outwash-drawdown pond (similar to coastal plain ponds), with *Fimbristylis autumnalis* (L.) R. & S. and *Rhexia virginica* L., both at range limits here. The limestone hills of Pownal, with the largest concentration of rare plants in Vermont, were also protected in this manner. In 1988, The Nature Conservancy secured partial protection of a site for Vermont's endemic maidenhair fern, a recently discovered taxon with twice as many chromosomes as the typical maidenhair.

The government of the State of Vermont has also increased its plant protection efforts as a direct consequence of new information. The island where *Lathyrus ochroleucus* Hk. was discovered, now a state park, has been developed with utmost care for the protection of the 17 rare species found on the island. Trails are routed away from rare plant populations and use will be limited to primitive recreation. Rare high-elevation cliff plants in Smuggler's Notch are now better protected by informational posting in the notch (a favorite place for rock climbers), a cooperative effort of the Heritage Program and Department of Forests, Parks and Recreation. In addition, at least 40 other rare plant sites on state land are receiving protection that they never had prior to the new wave of information and cooperation. Natural areas protection by the State of Vermont has been important for some time, but only recently has full protection become possible, as information and resources have become readily available.

Another important indication of the resurgence of interest and activity with respect to rare plants was the publication in 1986 of Joint Bulletin No. 20 of the Vermont Botanical and Bird Clubs.

The cover pages of the early Bulletins read: "Published annually by the Clubs"; the recent Bulletin reads: "Published at intervals by the Clubs." In fact those intervals had increased from an average of two years to thirty years between the last Bulletin of 1956 and the present 1986 Bulletin. The Botanical Club had always had a special interest in the unusual flora of the state, and in its early days had a very distinguished membership, including such people as Nellie Flynn, Ezra Brainerd, and Cyrus Pringle. Annual meetings continued uninterrupted through the years, but active interest in the rare flora of the state had diminished, as indicated by the absence of Club Bulletins. The Club and its members are now, again, actively involved in the research and protection of rare plants.

Perhaps the most important change of the decade was the 1982 amendment of the Vermont Endangered Species Act. The amendment represented an attempt to provide for updating of the lists and to establish sound management policies for endangered species, while at the same time making Vermont eligible for federal endangered species funds. Unfortunately the 1982 amendment was still flawed, and had to be revised again. Nevertheless, it provided for the establishment of an Endangered Species Committee, which worked ardently for two years to prepare new lists of endangered and threatened species, while the legislature worked to amend the law. The new amendments were passed in 1986 (10 V.S.A. Chap. 123), and the new lists adopted in 1987. Vermont now has an endangered species law which provides for protection and management of threatened and endangered species, and provides for the regular updating of the lists of protected species. Twenty-one plants are listed as Endangered, and 91 are Threatened.

The new age of comprehensive knowledge and viable legislation is represented well by the case of *Anemone multifida* Poir. This is a plant of moist river ledges that is at its southern range limit here and is rare throughout New England and New York. Four stations for this species have been known or reported in Vermont, but two are apparently extirpated. The plant has always been considered rare in the state, but clearly never received the protection that it deserved. In 1986, a hydroelectric developer submitted applications for the permits necessary to develop Winooski Falls, the largest remaining station for *A. multifida* in Vermont. The Endangered Species Committee, acting under authority of

the new Endangered Species Law, considered the proposal and met with the developer to discuss potential damage to the plants. An agreement was reached whereby the developer would minimize the disturbance so that only a small percentage of the *Anemone* population would be lost and an in-depth study and recovery plan would be prepared, funded by the developer and supervised by the Agency of Natural Resources. This agreement, made in a spirit of cooperation and mutual concern for the rare plants, represents a milestone of change from the early days when, only a mile upstream, *Astragalus robbinsii* (Oakes) Gray was lost forever because there was no provision for its protection.

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# MASSACHUSETTS FLORA: A REVIEW OF CURRENT DISTRIBUTION AND CONSERVATION OF RARE SPECIES

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The last time the New England Botanical Club held a symposium, in 1979, my botanical predecessors presented a paper on the status of rare vascular plants in Massachusetts (Field and Coddington, 1980). At the time of the symposium, intensive inventories such as those conducted by Natural Heritage Programs were just getting started. Much has happened since then, as we have already learned today. Although Massachusetts had been heavily botanized for over a century and a half, information on the distribution and abundance of rare species was scattered, out of date, and woefully inadequate in terms of directing protection priorities.

The Massachusetts Natural Heritage Program was begun in 1978 to inventory the state's rare flora, fauna, and plant communities. Limited fieldwork conducted up to and including 1978 had verified current occurrences for 37% of the taxa on the state list of rare plants (Coddington and Field, 1978). Since then, ongoing fieldwork has raised the figure to 80%. Progress in reverifying rare species was rapid for several years (about twenty species reverified per year), but since 1985 the rate at which "missing" species are found has dropped markedly (less than seven per year).

Forty-five species from the original Coddington and Field list (1978) have been removed from the list due to abundance, taxonomic decisions, etc. Conversely, forty-three taxa have been added to the list, based on current assessment of rarity (Sorrie, 1987b). Ten of those species are new discoveries to the state: *Woodsia glabella, Trichomanes* gametophyte, *Thuja occidentalis, Carex castanea, Carex chordorrhiza, Eleocharis microcarpa, Rhynchospora capillacea, Juncus debilis, Hydrastis canadensis,* and *Desmodium humifusum.*

The Natural Heritage Program database now contains 3000 occurrences (= "stations") of 241 rare plant taxa. A map of Massachusetts rare plant occurrences by town shows concentrations in the dolomitic limestone region and the Housatonic River Valley of Berkshire County; the traprock, sandstone, and conglomerate ridges and floodplain habitats in the Connecticut River Val-

ley; and in the Coastal Plain ponds, pine barrens, heathlands, and maritime habitats of southeastern Plymouth County, Cape Cod, and The Islands. Out of 351 towns and cities statewide, 160 support one or more current sites for rare plants; an additional 135 have historical sites only. Areas having few or no rare plant sites are indicative of relatively uniform topography and "ordinary" geology, rather than of less fieldwork. Towns with the most *occurrences* of rare species are in the three areas listed above. Those with the largest *number* of rare species (current and historical) are: Sheffield—50, due to its extraordinary diversity of calcareous ledges and fens, floodplain habitats, and rich mesic forest; Nantucket—43, due to its combination of heathlands, Coastal Plain wetlands, and barrier beaches. Stockbridge and Williamstown follow with 37 and 36 species, respectively. As a county, Berkshire far outdistances the others with 113 species, owing primarily to its extensive deposits of calcareous bedrock.

Major rediscoveries of the state's "missing" rare flora since 1979 have been numerous, because of dedicated efforts by many knowledgeable volunteers. Also, an ecologically enlightened citizenry has meant that many natural areas have been spared the developer's plow. Many of the rediscoveries up through 1984 have been documented in *Rhodora* (Sorrie, 1987a) and so today I will highlight some of those and bring us forward through the 1987 field season. In taxonomic order they are: *Polystichum braunii* on Mount Greylock, *Elymus mollis* in Gloucester, *Carex davisii* in Sheffield, *Carex livida* in Lynnfield, *Carex polymorpha* in Duxbury, *Eleocharis tricostata* on Nantucket, *Scirpus longii* in Dartmouth, *Scleria triglomerata* in Northbridge, *Chamaelirium luteum* in Sheffield, *Cypripedium arietinum* on Mount Toby, *Platanthera cristata* in Bristol County, *Triphora trianthophora* in Rowe, *Cardamine douglassii* in Sheffield, *Rosa acicularis* in Lanesborough, *Hypericum* (*Ascyrum*) *hypericoides* on Nantucket, *Pyrola asarifolia* in Berkshire County, *Halenia deflexa* in Cummington, *Hydrophyllum canadense* in North Adams, *Blephilia ciliata* and *B. hirsuta* in Berkshire County, *Agalinis acuta* on Cape Cod, *Lonicera hirsuta* in Williamstown at the type station, *Gnaphalium purpureum* on Nantucket, and *Solidago glutinosa* ssp. *randii* in southwestern Berkshire County.

Since the 1979 NEBC symposium, major phytogeographic finds within Massachusetts, in addition to the ten newly discovered species, include *Equisetum variegatum* from Norfolk and Worces-

ter Counties, *Milium effusum* from Franklin County, *Scirpus pendulus* from Bristol County, *Scleria pauciflora* from Cape Cod and The Islands, *Isotria medeoloides* from Hampden, Worcester, and Essex Counties, *Moehringia* (*Arenaria*) *macrophylla* from Berkshire County, *Cardamine longii* from Plymouth County, *Vaccinium vitis-idaea* and *Blephilia hirsuta* from northern Berkshire County, and *Symphoricarpos albus* from Franklin County.

Land use statistics show that Massachusetts has far more forested land today than 150 years ago, despite the building boom. Rare species reflect this trend. Of the 43 taxa which today are considered extirpated from the state, at least 31 inhabit early successional environments, habitats which were widespread across the state when most botanical collecting was done. Analyses of whether "missing" species are of northern, southern, or western biogeographical affinities have been inconclusive and show no definite trends, which is to say that there appears to be an across-the-board loss of species, regardless of geographical origin. Similarly, of the ten new species discovered in the state, five may be classed as northern and four as southern.

Since the inception of the Natural Heritage Program, we have come a long way in terms of recognizing what are the most important plant communities in the state, where they are located, and how they are threatened. At the top of the list are the coastal heathlands of Nantucket, the alkaline fens of Berkshire County, the Coastal Plain ponds of Plymouth and Barnstable Counties, and pine barrens wherever they are. We continue to actively search out areas of ecological importance as the key to the survival of rare taxa.

Turning to protection activities, there are four basic strategies employed. First, the Natural Heritage Program is part of the statewide environmental review process, coordinated by the MEPA (Massachusetts Environmental Policy Act) and DEQE (Department of Environmental Quality Engineering, which administers the state Wetlands Protection Act) offices. Comments are prepared on over 1400 development projects annually, resulting in various amounts of mitigation but rarely leading to land aquisition or conservation easements. In the absence of any statewide legislation which specifically protects plants, the environmental review process is a positive step toward protection.

Second, the Natural Heritage Program operates a Public Reg-

istry Program, which informs federal, state, and municipal agencies of rare species sites and works with them toward protection via habitat management, designation of unique natural areas, and inclusion of sensitive areas in long range planning documents. Some 170 properties have been targeted and are in various stages of implementation.

Third, The Nature Conservancy operates a Private Registry Program, which informs private landowners of rare species sites that have been identified by the Natural Heritage Program. To date 93 sites across the state have been protected, using a broad spectrum of protection techniques ranging from verbal agreements by the landowners to outright purchase of the parcel. Follow-up visits by TNC or MNHP staff help ensure that landowners are fully aware of our interest and commitment, and at the same time allow us the opportunity to negotiate for the level of protection deemed necessary for each parcel. As land prices have soared in the state, these two Registry Programs have become essential tools in rare species conservation.

Fourth, there is now in place a tax checkoff system in Massachusetts. For five years generous citizens have contributed money to a nongame wildlife fund administered by the Division of Fisheries and Wildlife. These monies have been and will be used primarily to purchase rare species habitat and to fund research on rare species through a Small Grants Program. A half-million dollars was raised during the 1986/87 tax season.

Through these various efforts, 182 rare species now enjoy some form of protection in the Commonwealth. This number represents 92% of the species for which we have current stations. However, in many instances we have not progressed beyond landowner contact; our goal now must be to afford these species stronger protection wherever possible via land acquisition and designation of unique natural areas.

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# PLANT CONSERVATION CONCERNS IN RHODE ISLAND—A REAPPRAISAL

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In 1978, the United States Fish and Wildlife Service published *Rare and Endangered Vascular Plant Species in Rhode Island,* authored by George Church and Richard Champlin. A total of 120 species were listed in the publication using the criterion of "rare" to mean five or fewer field stations. The list was initially derived through analysis of specimens housed at the herbaria of the New England Botanical Club and Brown University with further revisions based on field investigations.

Using the Church and Champlin list as a basis for study, along with subsequent publications including that of Stuckey (1979), a joint venture was initiated in 1979 between The Nature Conservancy and the Rhode Island Natural Heritage Program of the Department of Environmental Management to document the distribution of rare native vascular plants in the state. This effort, now in its 9th year, has been instrumental in deriving a clearer picture of the state's uncommon flora. Currently, 263 species and subordinate taxa are being tracked by the Natural Heritage Program. This list includes plants under the following designations:

**State Endangered** (53 taxa). Defined as native taxa in imminent danger of extirpation from Rhode Island under the following criteria:

1. A taxon currently listed or proposed by the U.S. Fish and Wildlife Service as Federally endangered or threatened.
2. A taxon with 1 or 2 known or estimated total occurrences in the state.
3. A taxon apparently globally rare or threatened, estimated to occur at approximately 100 or fewer sites range-wide.

The 53 taxa defined under this category are currently listed under the Rhode Island State Endangered Species Act, and thus receive protection from widespread collection.

**State Threatened** (60 taxa). Native taxa which are likely to become state endangered in the future if current trends in habitat loss or other detrimental factors remain unchanged. These taxa meet one or more of the following criteria:

1. A taxon with 3 to 5 known or estimated occurrences in the state.
2. A taxon with more than 5 known or estimated occurrences in the state, but especially vulnerable to habitat loss.

**State Interest** (65 taxa). Native taxa not considered to be state endangered or threatened at the present time, occurring at 6 to 10 sites in the state.

**Special Concern** (39 taxa). Taxa which do not qualify under other categories but are additionally listed due to various factors of rarity and/or vulnerability.

**State Extirpated** (46 taxa). Taxa which have been documented for the state during the last 100 years, but for which no current occurrences are known.

The increase in the number of species listed as endangered, threatened, or otherwise uncommon, is partially due to more comprehensive work on less studied taxa, especially the Cyperaceae with 24 newly listed species including four recently discovered additions to the state flora. These species are:

*Carex walteriana* Bailey (*Rawinski & Raithel 7899,* NEBC)
*Scirpus longii* Fern. (*Rawinski, Enser & Caljouw 6832,* NEBC)
*Scirpus etuberculatus* (Steud.) Kuntze (*Raithel s.n.,* NEBC)
*Scleria pauciflora* Muhl. (*Caljouw, Enser & Zaremba 87-342,* NEBC).

## DESCRIPTION OF INVESTIGATIONS

Initially, the Natural Heritage Program prepared a list of target plant species based on information garnered from previously published materials. Further analysis of herbarium specimens and discussions with knowledgeable botanists refined the list allowing a prioritization of field efforts. Initial field time was spent relocating historic stations which also aided in the identification of important plant community types which should be investigated for new records. These communities targeted as important rare plant habitats are assembled into two major groups based on their regional distribution and significance. Following are brief descriptions of these community types and highlights of those special plants found in each.

## GROUP I. REGIONALLY IMPORTANT PLANT COMMUNITIES AND RARE PLANTS

Community types considered important within the southern New England region, containing associations and species which are rare throughout the region, and also includes species rare rangewide. These types with primary examples are as follows:

### A. Coastal Plain Pondshores

Original identification of coastal plain pondshores was made in the early 1900's by regional botanists including J. F. Collins and M. L. Fernald. Characteristic species such as *Sabatia kennedyana* Fern., *Coreopsis rosea* L., and *Sagittaria teres* S. Wats. are documented in herbaria from stations in Providence and Kent Counties during this period. These sites, the most notable of which was Gorton's Pond in Warwick, have been highly impacted by urbanization and heavy recreational use and no longer serve as viable habitats for these species. In addition, brief forays by these noted botanists into Washington County unveiled other locations for coastal plain species. Pondshores supporting these rare species occur on moraine and outwash plains less than 10 miles inland from the Atlantic Ocean. These early indications of potentially important habitats served as a guide for recent surveys, including a report by Sorrie (1981) regarding the distribution of *Eupatorium leucolepis* var. *novae-angliae* Fern., an endemic to southern New England. Additional work, including that of G. Tucker (pers. comm., 1979), served as a basis for Natural Heritage Program surveys over a wider portion of the Washington County area.

The Matunuck Hills area, consisting of ten small ponds on approximately 1200 acres of the Charlestown recessional moraine, is the state's best example of this important community and rare plant habitat. The seasonally fluctuating water levels of these freshwater ponds provide the ephemeral sandy shorelines required for the emergence of many rare plants. Rare taxa documented from this area include *Sagittaria teres* S. Wats., *Eleocharis tricostata* Torr., *Fuirena pumila* Torr., *Psilocarya scirpoides* Torr., *Rhynchospora macrostachya* Torr., *Scleria reticularis* Michx., *Hypericum adpressum* Barton, *Coreopsis rosea* L., *Eupatorium leucolepis* var. *novae-angliae* Fern., and *Scirpus etuberculatus* (Steud.) Kuntze. *S. etuberculatus* was first documented

in Rhode Island at this site in 1986 and is a major disjunction from the next closest station to the south on the Delaware coastal plain.

Additional coastal plain ponds in Washington County include Worden's Pond in South Kingstown and Deep Pond in Charlestown where the state's only current sites for *Sabatia kennedyana* L. and *Orontium aquaticum* L. are located.

Several key tracts in the Matunuck Hills area have been permanently protected through the combined efforts of The Nature Conservancy, The South Kingstown Land Trust, The Audubon Society of Rhode Island, the State, and the Town of South Kingstown.

**B. Coastal Plain Quagmires**

A second community type, seemingly coastal plain in distribution, occurs at wetlands characterized by stable water levels throughout the growing season and loose mucky or peaty substrates. Most of these ponds/wetlands are associated with *Chamaecyparis thyoides* (L.) BSP. swamps which maintain the constant water supply. Unlike open water areas associated with bogs, quagmires occur as shallow water areas with well defined emergent plant zones which are represented by two uncommon species, *Rhynchospora inundata* (Oakes) Fern., which is currently known from 4 sites in the state, and *Eleocharis equisetoides* (Ell.) T.

The distribution of *E. equisetoides* is of particular interest regionally. Historically recorded from approximately 5 sites in New England, including Massachusetts, Connecticut, and Rhode Island, only one site is extant in Connecticut, (L. Meyrhoff, pers. comm.), and none from Massachusetts. A total of 7 sites have been located in Rhode Island during the past three years. Distributed in three counties, these sites align along the western border of the state in the region underlain by a Hope Valley Alaskite Gniess bedrock. The reason for the apparent affinity of *E. equisetoides* to this geologic formation is not currently understood.

**C. Morainic Grasslands**

The distribution of this community type is limited to Block Island. This island, lying 12 miles south of the mainland, presents

an interesting puzzle on plant distribution. It is evident that large portions of the island were forested historically, based on observations of early historians and recent fossil pollen investigations, but major stands of woody vegetation were eliminated early in the island's settlement to provide fuel and building materials (Livermore, 1877). By the middle of the 18th century the island was converted into a vast agricultural plain, used primarily for grazing, with barely a tree visible on the landscape. Although the lack of historic information leaves much to conjecture, it is probable that some plants such as hickories and tree oaks were lost from the island due to this major alteration of the habitats (P. Dunwiddie, pers. comm.). Moreover, the relatively small size of the island which inhibits chance establishment of species, and the lack of habitat complexity results in a generally depauperate flora at the present.

The most noteworthy community type found on Block Island is the morainic grassland, areas of relatively small size (usually less than ½ acre) which are generally limited to the exposed and xeric southeastern bluffs and hillsides where aggressive woody shrubs such as *Myrica pennsylvanica* Loisel. and *Viburnum dentatum* L. have failed to become established. These dry, sandy knolls serve as habitat for *Helianthemum dumosum* (Bickn.) F., *Aristida purpurascens* Poiret, *Polygala nuttallii* T. & G., and New England's only occurrence of *Chrysopsis mariana* (L.) Ell.

**D. Acid Fens and Atlantic White Cedar Swamps**

This significant coastal plain habitat located at the Great Swamp Wildlife Management Area in South Kingstown appears most similar to peatland communities found in the New Jersey pine barrens. The Great Swamp peatland appears in linear patterns of sedge-dominated vegetation interspersed with linear groves of *Chamaecyparis thyoides* (T. Rawinski, pers. comm.). The globally rare *Scirpus longii* and state endangered *Carex walteriana* were recently discovered here and occur as dominants along with *Carex exilis* Dew. in open fen areas. Cool, dark, and mossy *Chamaecyparis* groves provide habitat for the elusive *Carex collinsii* Nutt. at its only Rhode Island station. The area is protected as a state wildlife management area and the Heritage Program has made management recommendations for the area's long-term preservation.

### E. Pitch Pine and Scrub Oak Barrens

Several thousand acres of this community type occur in Rhode Island, primarily within Kent and Washington Counties on sandy outwash soils. Dominates include *Pinus rigida* Mill., *Quercus ilicifolia* Wang., and *Q. prinoides* Willd. with the percent cover of each dependent on the fire and disturbance history at each site. Unusual state rare plants found in dry grassy openings within the barrens include *Lupinus perennis* L., *Tephrosia virginiana* (L.) Pers., and *Linum intercursum* Bickn. Although these areas are often lacking in high plant diversity, occasional small wet depressions or seeps can be found which support rare coastal plain flora. A recently located site of this description in Charlestown supports a wide diversity of species including the state endangered *Scleria triglomerata* Michx., *S. pauciflora,* and *Rhynchospora torreyana* Gray.

## GROUP II. STATE IMPORTANT PLANT COMMUNITIES AND RARE PLANTS

Community types considered important in Rhode Island, containing associations and species rare within the state.

### A. Calcareous Woodlands and Outcrops

Calcareous communities are restricted primarily to the town of Lincoln where unique plants have become established in an area associated with a relatively small outcropping of dolomitic marble. Diverse assemblages of plants thrive on marble ledges and in rich woods on fertile soils derived from the area's calcium-rich bedrock. This area serves as the only documented location statewide for calciphytic species including *Asplenium rhyzophyllum* L., *Pellaea atropurpurea* (L.) Link, *Galearis spectabilis* (L.) Raf., and *Parnassia glauca* Raf. along with other rare associates *Liparis lilifolia* (L.) Rich ex Lindl., *Platanthera hyperborea* (L.) Lindl., and *Actaea rubra* (Ait.) Willd. The area's unique flora has been well-documented since the turn of the century, and recent acquisitions by The Nature Conservancy will help in preserving one of the state's most botanically rich natural areas.

### B. Acid Level Bogs

In Rhode Island, peat bogs occur at kettle holes, small depressions, or rarely as floating mats within larger bodies of water. This community supports species which are more commonly distributed in northern areas, but are considered rare in Rhode Island at the southern edge of their range. A primary example is the Bowdish Reservoir floating peat islands in Glocester which is the only station in the state for *Arceuthobium pusillum* Peck, *Kalmia polifolia* Wang., and *Andromeda glaucophylla* Link. The state has recently secured protection of the reservoir's shoreline, thereby protecting the floating islands.

## ADDITIONAL RARE PLANTS

With the use of aerial photographs, soil, geologic, and topographic maps, communities such as calcareous forests, acid fens, bogs, coastal plain quagmires, and pitch pine barrens can be systematically identified and field checked for rare plant occurrences.

Field investigations are more difficult for those rare species which do not readily align themselves with a particular community type. *Agalinis acuta* Pennell is an example of such a species. Historically noted from five sites in Rhode Island, this globally rare species, now proposed for Federal listing, was last observed in Cumberland in 1941 (*E. J. Palmer s.n.*, NEBC). Its habitat appears to be sandy *Schizachyrium scoparium* (Michx.) Nash grassy openings. Recent intensive field surveys have proven unsuccessful; however, surveys will continue as much suitable habitat appears to remain for this elusive species.

Another species which has evaded field surveyors for many years is *Platanthera ciliaris* (L.) Lindl. Historically known from several occurrences in Washington County, the preferred habitat appears to be seasonally wet meadows, usually in association with *Aletris farinosa* L. Following a ten-year hiatus in records this species was reconfirmed in 1988 at one site in South Kingstown which is an active Christmas tree farm. Efforts are now proceeding to work with the private landowner to protect this rare orchid.

The globally rare *Carex polymorpha* Muhl. was historically known from two sites in Rhode Island, last seen in Barrington in 1911 (*M. L. Fernald, s.n.*, NEBC). A new record was discovered

in 1988 in the town of North Smithfield (T. Rawinski, pers. comm.). Again, the habitat for this species is difficult to characterize, but it appears to be found in seasonally wet meadows on fragipan soils.

## PROTECTION OF RARE PLANTS

Approximately 50% of the 112 species listed under state endangered and threatened categories occur on sites which are considered to be protected by federal, state, town, and private conservation organizations. The level of protection afforded these sites varies with the goals of the managing agency. An important component of these protection efforts has been the Natural Areas Registry Program initiated in 1983 as a cooperative effort of The Nature Conservancy and the Natural Heritage Program. The Registry Program is designed to enlist the voluntary cooperation of private and public landowners in protecting significant natural areas. State endangered plants and threatened plant habitats have been a priority for protection from the onset. To date, as many as 60 landowners have agreed to protect important botanical resources found on their property.

Significant strides in land acquisition to protect rare and endangered plants were afforded through the state Open Space Bond Program. In 1985 and 1987, the voters of Rhode Island passed two bond referenda which provided over $19 million for open space acquisition. This money is allocated as grants to municipalities, private conservation groups, and land trusts through an application process. Applications are reviewed by the Natural Heritage Preservation Commission and ranked according to a set of criteria which assess the natural values of land covered under an application. One criterion is the presence of rare and endangered species for which the Natural Heritage Program's list of target species and data base are used as the basis for making decisions. The Program also reviews the required management plans for areas, once they are protected by open space grants, to insure that proper stewardship is employed to maintain habitats identified for rare species.

Additional protection for rare plants is provided through State freshwater and coastal wetlands legislation. Approximately 50% of the species listed as state endangered and threatened are those

found on inland wetland habitats which fall under the scrutiny of the Rhode Island Freshwater Wetlands Act. This legislation mandates that alterations to wetlands shall require a permit, the allocation of which is governed by stringent regulations which identify the values associated with particular wetland sites. Larger wetlands are insured protection under this program, and sites may receive additional safeguard if identified as "unique," the designation of which is based on several important values including the presence of species identified by the Natural Heritage Program.

Similar protection is also afforded by the Coastal Resources Management Act to plants in estuaries, dunes, and other coastal habitats.

## SUMMARY

For the past several years a tremendous amount of field work has been directed toward Rhode Island's rare and endangered plants. Many individuals have contributed their observations to the Natural Heritage Program data base, making it the largest and most comprehensive repository of rare and endangered plant information in the state. As new information is provided and studies continue, this evaluation of the state's flora will attain greater precision.

The following is a partial list of Natural Heritage Program contacts whom we would like to acknowledge for their contributions to this dynamic process: Julie Lundgren, Thomas Rawinski, Christopher Raithel, Irene Stuckey, Gordon Tucker, Frank Golet, Richard Champlin, Gilbert George, and Waldo J. Peepers.

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# INVENTORYING CONNECTICUT'S VASCULAR PLANT DIVERSITY

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## ABSTRACT

The Connecticut Geological and Natural History Survey has been sponsoring botanical inventories in Connecticut since its inception in 1903. In 1975 a field team was charged with beginning a statewide inventory of Connecticut's rare species of vascular plants and vertebrate animals; results of these inventories were published in 1976. This publication listed 274 vascular plant taxa as endangered, threatened, or otherwise of interest as uncommon plant species. In 1982 the Connecticut Natural Diversity Data Base was established as a program of the Connecticut Geological and Natural History Survey. The charge of the Data Base is both to accumulate and disseminate data on the biota of Connecticut with special attention being paid to Species of Special Concern. The Natural Diversity Data Base currently lists 331 vascular plant taxa.

Since 1979 the Survey has increased its field efforts to locate Species of Special Concern. In addition to a botanist, the Survey funds a full-time plant ecologist whose primary charge is to establish a biophysical land classification for Connecticut. Plant communities are being mapped on 1:250,000 base maps. The Survey also has responsibility for a land owner contact program called the Connecticut Natural Heritage Registry which uses rare species information obtained from the Natural Diversity Data Base.

Recent field work has yielded some interesting botanical finds. A number of historic records have been re-located, including *Cypripedium reginae, Petasites frigidus* var. *palmatus, Cryptogramma stelleri, Polygala senega, Polygala nuttallii,* and *Solidago rigidus.* New localities for *Trollius laxus* ssp. *laxus, Viburnum prunifolium,* and other species of concern have been found. One locality for a U.S. Endangered Species, *Isotria medeoloides,* is currently known in Connecticut. Some species new to Connecticut such as *Psilocarya scirpoides* have been located.

Research on *Moehringia macrophylla,* a species which occurs in Connecticut at two algific talus slopes, is briefly discussed as an example of new program directions.

## HISTORY OF STATE EFFORT

The Connecticut Geological and Natural History Survey vascular plant inventory began in 1903. On June 3 of that year, the state legislature established the State Geological and Natural History Survey, and charged it with inventorying and researching the geology and biota of the state. It had a board of commissioners and a paid, part-time superintendent, William North Rice of Wesleyan University. A few months earlier, in January, 1903, a group of interested gentlemen had formed the Connecticut Botanical Society (Eames, 1903). Shortly after the establishment of

the Survey, Rice approached the state flora committee of the Botanical Society actively working on a state catalog. This committee responded "most cordially to the suggestion that they find in the newly organized State Survey, a medium for the publication of the results of their labor" (Rice, 1904).

It was not until 1974 that the Survey hired its first full-time biologist, Joseph Dowhan. He was charged with identifying the rare flora and fauna of Connecticut and their habitats. Dowhan, together with his field team of R. J. Craig and L. J. Mehrhoff, spent the next two years in this preliminary study. The results of this initial effort were published by the State Survey in 1976 as a Report of Investigations entitled, *Rare and Endangered Species of Connecticut and Their Habitats* (Dowhan and Craig, 1976).

In 1978, Dowhan left the Connecticut Geological and Natural History Survey and I replaced him as the head of the Survey's biology program. At that point the primary interest shifted to botanical field work. We also hired a second biologist, a plant ecologist, Kenneth J. Metzler, to assist in the inventory.

The *Rare and Endangered Vascular Plants of Connecticut* was published in 1978 in conjunction with the New England Botanical Club's Rare and Endangered Species committee, with financial support of the U.S. Fish and Wildlife Service (Mehrhoff, 1980).

In 1982, the Survey entered into a memorandum of understanding with the Connecticut Chapter of The Nature Conservancy to form the Connecticut Natural Diversity Data Base. The Data Base employed the Conservancy's Heritage Program methodology to manage data in a computer-assisted topographic mapping program. This kind of data base is used for storing and retrieving data so they can be used for land use decision making needs (Jenkins, 1978, 1981). This data base gave us a mechanism for making our data available to the public. Nancy M. Murray was hired to manage these data and to handle requests for information. Currently, we have over 2500 occurrences of both Species of Special Concern and natural communities on our maps.

We have gone one step further with our natural communities. Each community type is mapped on separate 1:250,000 scale maps, giving us the capability to scan the state quickly to see distribution of a particular habitat type. This capability is especially helpful when looking for rare plants which have specific habitat requirements. Using a system of open and closed circles

allows us to tell at a glance whether or not we have any information on a particular site.

The Connecticut Geological and Natural History Survey currently maintains a list of 331 vascular plant taxa that we consider Species of Special Concern. Additional taxa are being considered for inclusion, other species are being reviewed for possible deletion.

Embarrassingly, Connecticut currently has no endangered species legislation. (There is strong reason to believe that this void might be filled after the next legislative session in Connecticut.) The embarrassment is exacerbated by the fact that Connecticut was probably the first state to pass legislation to protect a plant species of aesthetic nature (Eaton, 1879; Mehrhoff, 1980).

Connecticut, for a small state of 5009 square miles, exhibits remarkable diversity. Over the past 15 years we have been fortunate in identifying critical localities for many of our less common taxa. We are also fortunate in having partners in preservation such as the Connecticut Chapter of The Nature Conservancy who assist when we do locate a stand of a rare species. Again, in conjunction with The Nature Conservancy, we have established a landowner contact program called the Natural Heritage Registry Program. At present, work is under way to assure the long-term survival of many of our rare vascular plants.

## SPECIFIC TAXA DISCUSSIONS

We have been told elsewhere in this symposium by Dr. Hugh Iltis that true endemics should not exist in glaciated areas. Luckily, Gregory J. Anderson anticipated Iltis's comments and reduced Connecticut's only endemic species, Graves Beach Plum (*Prunus gravesii*), to a variety of the common Beach Plum (*Prunus maritima*). There are numerous data to support this position. *P. maritima* var. *gravesii* quite possibly might have arisen as a mutation which would explain this single population (Anderson, 1980).

The only U.S. Endangered Species of vascular plant currently known to exist in Connecticut is *Isotria medeoloides*. Until recent field work in New Hampshire and Maine yielded such good results, Connecticut had the highest number of historic localities. Prior to 1970, *Isotria medeoloides* had been reported from seven

localities in the state. We have not been able to locate any of these stations. Our one current population was discovered after a newspaper article with an illustration ran in the Sunday edition of the Hartford *Courant*. Someone who had seen the plants in northwestern Connecticut a year earlier reported the locality to us. When we first visited the site in 1984, we found four plants and a squared-off hole where a fifth plant had been removed. In 1986, we could not find any plants at this site, but in 1987 we found another subpopulation of nine plants five meters from the location of the original site. Seven individuals were observed in 1988.

This hole where a plant of *Isotria medeoloides* had been removed is what prompted the Connecticut Geological and Natural History Survey to seek legislation making information in the Natural Diversity Data Base exempt from the Connecticut Freedom of Information Act. Section 24-2a of the General Statutes helps us protect our information by giving us the right to deny the request for Natural Diversity Data Base information unless good reason for its need is presented. To date, we have not had to use this capability.

In contrast, Connecticut has a number of sites for *Isotria verticillata*. Many of these localities are in eastern Connecticut; a few of the sites may have as many as 1,000 individuals.

The rest of Connecticut's Species of Special Concern may be more common elsewhere; an example is the three-toothed Cinquefoil, *Potentilla tridentata*. Although common in northern New England, Connecticut has only three stations, all found in the northwest uplands. There is a fourth locality along the Connecticut coast, but I question its naturalness at this site. It is in New Haven County, near Long Island Sound. The colony is healthy and appears to be spreading. This area was well botanized in the early part of the 20th century; no mention was ever made of *Potentilla tridentata* at this locality. The fact that it may not be native can perhaps be corroborated, because it does not occur along the Rhode Island coast (R. Enser, pers. comm.), and in Massachusetts it occurs as far south as Cape Cod, in sand (B. Sorrie, pers. comm.). If it is native at this site it would mean that the coastal Connecticut population constitutes a major disjunction. This interpretation is hard to accept especially since Long Island Sound's currents flow predominantly toward the open sea to its east.

The calcium carbonate region of western Connecticut has yield-

ed many interesting plants which, although possibly more abundant elsewhere, are rare in Connecticut. One of these plants is *Trollius laxus* ssp. *laxus.* There are currently five populations of this species in Connecticut, all in Litchfield County. Although we had looked for this taxon for a number of years, it was first re-located by us in May, 1979. Since then, we have located an additional four stations; at two of these sites, it is locally abundant. It appears that individuals do not flower every year.

*Petasites frigidus* var. *palmatus* is another calciphile found in the wetlands of Litchfield County's limestone region. Although historic records existed, this plant was not re-located until 1981. We currently know of five stations.

Another calcareous wetland species that has recently been re-located in northwest Connecticut is *Cypripedium reginae,* first re-located by Caren Caljouw in 1982 while working as a Natura Conservancy intern. Caren convinced the Connecticut Chapter that in order to best understand their limestone fen preserves in this region she had to look at as many calcareous wetlands as possible. I think Caren doubled our knowledge of the current calcareous wetland flora that summer. *Cypripedium reginae* was thought to have been extirpated from northwest Connecticut by wildflower gardeners. We currently have three stations for this species; only one of these sites is protected at present.

*Rhynchospora capillacea* was first found in Connecticut in 1910 and had not been collected again until 1982. In Connecticut this northern calciphile is now known from two disturbed localities. The clue to locating additional stands may be to look in disturbed wetlands with exposed calcareous soils.

*Selaginella eclipes,* a midwestern species, was first discovered to exist in northwestern Connecticut by Dr. Terry Webster from the University of Connecticut. This taxon closely resembles *S. apoda* and he noticed a misidentified specimen in the University of Connecticut Herbarium (CONN). We began to search suitable habitats in Connecticut's limestone region and found three localities for *Selaginella eclipes,* but we were not able to re-locate the original population in Ridgefield. The best stand of this taxon was found in 1982 on the damp floor of a then abandoned limestone quarry. That site has since been destroyed by reactivation of the quarry. There are taxonomic questions about the validity of this species which need to be addressed.

Until recently, *Polygala senega* was only known from one his-

toric locality in Connecticut, where it was last collected in 1933. With a search image gained on the Spring 1987 New England Botanical Club Field Trip to Burlington, Vermont, we were able to go to the old locality in Litchfield County and relocate the Connecticut population. There are over 500 plants on a dry limestone ridge. Other species of note at this site are *Quercus muhlenbergii, Linum sulcatum, Asclepias verticillata, Onosmodium virginianum, Liatris borealis,* and *Solidago rigidus. Taneidia integerrima* was also reported from this locality in 1900 but has not been relocated.

Rare pteridophytes are well represented in the marble regions of western Connecticut. *Asplenium ruta-muraria* is currently known from five localities. *Cryptograma stelleri* eluded us until recently when we re-located a small population near a limestone seep.

A habitat which is well represented in Connecticut is *Sphagnum* bogs. Many of these bogs are actually quite different from one another and the species composition of many of them is also very different. A number of Species of Special Concern are found in the State's sphagnous bogs or acidic fens. Interestingly, many of the bogs support different assemblages of rare species than ones nearby. *Andromeda glaucophylla* is known from six localities in the state as is *Eriophorum spissum. Ledum groenlandicum* occurs at four sites. Historically *Scheuchzeria palustris* occurred in at least six localities; currently it is only known from one sphagnous bog in Connecticut. All these bogs occur in the northern half of the state.

A bog species that has an interesting distribution in southern New England is dwarf mistletoe, *Arceuthobium pusillum.* In Connecticut it is extant at two localities in one town. It had also been collected at two other bogs in nearby towns in the northwest corner; it has not been collected elsewhere in Connecticut. Interestingly, it occurs in Rhode Island less than a mile from Connecticut's eastern border.

The Hartford Fern or Climbing Fern, *Lygodium palmatum,* was apparently abundant in the central valley and in the ecologically similar sites in the southeastern uplands. We have at least 31 historic localities for *L. palmatum* in Connecticut. This species had suffered from both habitat destruction and over-collection. Collection pressure in Connecticut was so heavy the 1869 Law was passed (Eaton, 1879). Now the rapid urbanization of Con-

necticut's central valley precludes the possibility of many additional localities being found. The extensive stands in the state occur in Windham County. There are eight extant populations currently known from Connecticut; only three appear to be flourishing.

*Rhododendron maximum* can be found in a variety of habitats in Connecticut. It currently occurs on three wooden rocky slopes in Litchfield County. It has been reported from one swamp each in Fairfield, Windham, and Tolland Counties; in New London County it occurs in a few wetlands, usually as an understory dominant in stands of Atlantic White Cedar (*Chamaecyparis thyoides*). It has not been reported from Hartford, New Haven, and Middlesex Counties.

*Minuartia glabra* (= *Arenaria groenlandica* var. *glabra* (Fernald, 1950)) has an interesting distribution. It occurs both on the coast and inland in Maine, on a few mountain tops in north central New Hampshire, and has not been reported from Vermont and Massachusetts. In Rhode Island it occurs on a few rock outcrops in Washington County. It also occurs to the west of Connecticut in the Schwangunk Mountains and Catskill region of New York (Fernald, 1917; Seymour, 1982). In Connecticut, it occurs on pegmatite outcrops in Middlesex County (Harger et al., 1930). It occurs predictably on many pegmatite outcrops in this region.

*Liquidambar styraciflua* reaches the northern limit of its range in southwestern Fairfield County. We know of five sites where we feel reasonably confident that it is native. We have recently noticed that another Connecticut rarity, *Viburnum prunifolium,* occurs as an associate with *Liquidambar.* Currently, we know of four stations for this species in southwestern Connecticut.

Both *Liquidambar styraciflua* and *Viburnum prunifolium* are species which commonly occur in New Jersey's piedmont region. It is interesting to speculate as to the possibility of a northern extension of the piedmont into Southern New England. No hard data exist to support this hypothesis at present.

Another southern taxon reaching the northern limits of its distribution in Connecticut is *Floerkea proserpinacoides.* We have two extant localities, both on alluvial floodplains in southwestern Connecticut. This species is so ephemeral that it is conceivable that more populations exist. Historically, it occurred at six localities in Connecticut.

The persimmon, *Diospyros virginiana,* is another southern tax-

on which occurs along Long Island Sound. There have always been questions about the nativeness of *Diospyros* at its one Connecticut site near New Haven. Graves et al. (1910) in *Catalogue of the Flowering Plants and Ferns of Connecticut* state, "This station is said to have been known as early as 1846." They go on to question whether or not it might have been introduced by man. If it is native, it represents the northeastern limit of its distribution (the populations on Cape Cod are known to have been introduced after a shipwreck (P. Rich, pers. comm.; B. Sorrie, pers. comm.)). It also occurs at scattered localities, where it is thought to be native, around Long Island Sound in New York (J. Beitel, pers. comm.). From a preservationist point of view its nativeness in Connecticut is now a moot point. This once abundant species (1899 photographs, Connecticut Geological and Natural History Survey archives) has dwindled to a single staminate individual. As a dioecious species this taxon has been functionally extirpated from Connecticut.

Another southern element which occurs in Connecticut on the traprock (basalt) ridge system which bisects the state is *Corydalis flavula*. This species was historically known from three localities but had eluded us until 1981 when Bruce Tiffney and NEBC members re-located one of the populations. Learning the habitat for this species was important in re-locating the other two stations, which we did in 1983. *Corydalis flavula* is a spring ephemeral and most easily found when in flower at the end of April or early May.

*Muhlenbergia capillaris* is currently known from only one locality in southern Connecticut. It occurs here on exposed traprock ledges. Historically, there were four Connecticut stations. *Sporobolus heterolepis* also occurs at some of these sites.

Another southern species, disjunct in New England at one locality is the Hairy Lip Fern, *Cheilanthes lanosa*. It occurs on a shaded traprock ledge in southcentral Connecticut. *Cheilanthes* was originally found on West Rock, New Haven, Connecticut in 1892. Although it was not recognized as *Cheilanthes*, the specimen was taken to Daniel Cady Eaton at Yale who identified it as *Cheilanthes* and forwarded it for verification to William Davenport, another fern specialist with the Massachusetts Horticultural Society. We know from Eaton's correspondence where this plant had been found. The site was quarried some time in the early 20th century and the station destroyed. Our current station

was located in 1978 by B. G. Aiken (Aiken, 1980). This site was the first site to be registered with the State and The Nature Conservancy's Natural Heritage Registry.

Another interesting rarity of the basalt ridge system is the Prickly Pear Cactus, *Opuntia compressa.* One station is known from an open ledge on one of the southern traprock ridge tops. This species also occurs naturally along our coastline. *Opuntia* can be found at seven other coastal sites on sandy beaches or rocky headlands.

The coastal plain element of Connecticut's flora is well represented in spite of the fact that we have no coastal plain in Connecticut. Geomorphologically, Glacial Lake Connecticut separated the coastal plain on what is now Long Island from mainland Connecticut. We do have a number of ecologically similar habitats, however. Most of these occur in sandy deposits that formed as postglacial lake beds such as were formed by Glacial Lake Hitchcock. We look in these areas for our rare coastal plain taxa.

*Lachnanthes caroliana* presently occurs at only one locality. *Saururus cernuus* can be found at two stations. *Polygala nuttallii* occurs at one ecologically similar locality on a dry ridge in the central portion of our state. *Rhynchospora macrostachya* occurs at five localities. The diminutive *Hemicarpha micrantha,* although reported from six localities, can only be found on one pond shore where it was first discovered in 1984. Interestingly, although historic specimens average 2–6 cm in diameter, our extant plants are not much bigger than a dime. *Scleria reticularis* can be found at one station where it was first located in 1907.

*Psilocarya scirpoides* was located in 1983 along a pond shore in the northcentral valley of Connecticut (Mehrhoff, 1982). The water level at this pond draws down by the end of the summer, similar to the ponds of Cape Cod and southern Rhode Island. *Psilocarya* occurs along the exposed margins. In years of highwater (1984–85), we could not find this species; it was last seen at this site in 1987.

Perhaps the most striking coastal plain species in Connecticut is *Platanthera ciliaris,* the Yellow-fringed Orchid. Its only extant New England stations are in southern Connecticut, where we have six current sites. One of these, however, is unique. This station has been estimated to have over 5000 individual plants in a two-acre area. This appears to be the largest population of *Platanthera ciliaris* known. Current studies are underway to learn more about

this species' ecology. The site although vulnerable to adjacent agricultural land use is currently registered with the Natural Heritage Registry. The owner has managed this site for the enhancement of the orchid by mowing the area after the *Platanthera* has finished fruiting. This has kept the woody vegetation under control and possibly helped to disperse the seeds.

*Arethusa bulbosa* was once widespread in Connecticut. In 1982, we found two of our historic populations but one of these has not been seen since 1983.

Several rare species have been located along the Connecticut River. *Orontium aquaticum* can be found in a number of freshwater tidal marshes along the lower portion of the river; it also occurs in a few localities away from the Connecticut River. *Arisaema dracontium* can also be found in many of the remaining remnants of once-extensive flood plain forest. Like *Orontium,* it occurs in a few localities away from the Connecticut River, along the Housatonic and Pomperaug Rivers.

*Populus heterophylla* has been reported from three sites along the Connecticut River. Currently we know of its occurrence at only one of these sites. Two other stations are known, one in a swamp in south central Connecticut where only a few individuals still persist, and from one station surrounding a vernal pool near the summit of a traprock ridge, where it appears to be flourishing. It was first reported here in 1911 (Harger, 1913). *Salix exigua* (= *Salix interior* (Fernald, 1950)) the sandbar willow, is currently known from three localities along the Connecticut River. I fully suspect that it occurs in more localities but we must walk the available river shoreline in order to locate additional stations.

*Honkeyneya peploides* (= *Arenaria peploides* (Fernald, 1950)), common further north, occurs along the eastern portion of Connecticut's coastline. It does not occur west of Westbrook. One station for *Ranunculus cymbalaria* has been located at the edge of a saltmarsh in southeastern Connecticut. A southern grass, *Panicum amarum,* can be found at six localities in western Connecticut, although it has been reported as far east as East Lyme. Likewise, *Aristida tuberculosa* can now only be found along the Connecticut coastline in Fairfield County.

## FUTURE DIRECTION

As was stated earlier, Connecticut does not presently have the statutory authority to protect its rare flora or fauna. A bill is

currently being drafted that will correct this deficiency. Such legislative authority is of paramount importance to our efforts.

Inventory is still the primary function of the Connecticut Geological and Natural History Survey's Biology Program. In addition to cataloguing the flora and plant communities of the state, some research on rare plants is being conducted.

*Moehringia macrophylla* (= *Arenaria macrophylla* (Fernald, 1950)) occurs at two algific (ice-filled) talus slopes in southern Connecticut. Other sites in the northeast where this species occurs are on serpentine rocks. In Connecticut it occurs at the base of basalt ledges and talus slopes. The crucial difference is that ice forms in these slopes and persists well into the summer. I have found ice at one of the sites as late as the first of August. In addition, a number of taxa more typically found in northwestern Connecticut occur here as well. Temperature data (Mehrhoff, in press) indicate that the area at the base of these slopes remains much colder than the surrounding areas. This species is dispersed by ants (van der Pijl, 1982). Edward O. Wilson, of Harvard University, has suggested that I may find, with the *Moehringia,* species of ants not commonly found in southern New England. To date I have only observed two individuals, each of a different species (one *Camponotus pensylvanicus,* one not identified). Both sites are currently registered with the Natural Heritage Registry.

Dan Janzen has said that interactions between species and between species and their environment are the most important goals of protection (Janzen, 1988). By inventorying the flora and doing research of this nature we are trying to protect these interactions. Because we don't recognize many of the interactions at present, we can only strive to protect species' critical habitat. In a state facing the development pressures that Connecticut is currently facing, this will be no easy task. We are lucky to have the support of organizations like The Nature Conservancy, and of the many people in the state who believe in the preservation of Connecticut's Natural Heritage.

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# MAIDENHAIR FERN BIOGEOGRAPHY AND M. L. FERNALD'S HYPOTHESIS OF A GASPÉ REFUGIUM

CATHY A. PARIS

ABSTRACT

In his 1925 publication *The Persistence of Plants in Unglaciated Areas of Boreal America,* Fernald set forth his ideas about the biogeographical history of the plants of the Gaspé Peninsula. Noting the large number of taxa in that flora that, in his opinion, represented disjunct populations of western cordilleran species, Fernald suggested that these once-widespread species survived Pleistocene glaciation in the Gaspé on ice-free mountaintops called nunataks. Numbered among Fernald's western disjuncts was *Adiantum pedatum* L. var. *aleuticum* Rupr., a maidenhair fern he had discovered 20 years earlier on the serpentine tableland of Mt. Albert. Although subsequent geological and botanical evidence has cast doubts on Fernald's nunatak hypothesis, his association of the serpentine maidenhair with the flora of the western cordillera is probably correct. Results of recent cytological, morphometric, and electrophoretic studies of the *Adiantum pedatum* complex in North America indicate that var. *aleuticum* is more closely related to the maidenhairs of western North America than to the typical maidenhair of eastern woodlands. Probably the western component of the *Adiantum pedatum* complex extended its range eastward along a deglaciated corridor following retreat of the Wisconsin ice; isolated populations of var. *aleuticum* were left on serpentine following re-establishment of normal vegetation. Islands of serpentine substrate, not unglaciated terrain, provide refugia for this taxon in eastern North America.

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# NEW ENGLAND *CAREX* (CYPERACEAE): TAXONOMIC PROBLEMS AND PHYTOGEOGRAPHICAL CONSIDERATIONS

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## ABSTRACT

*Carex,* the largest genus of flowering plants in New England, has long presented systematists and floristicians with difficulties. An update on recent systematic research of New England *Carex* is presented and persisting areas of taxonomic difficulty are tabulated. Whether a species is northern or southern in overall distribution with respect to New England is suggested to be significant, with northern species more frequently persisting as isolated occurrences and under more threat than southern species.

Key Words: *Carex,* New England, phytogeography

## INTRODUCTION

With about 185 species (Seymour, 1982), *Carex* is the largest genus of vascular plants in New England. Sedges are an important element of most terrestrial communities throughout New England and are prominently represented in rare, threatened, and endangered species lists for all the New England states. However, the large size and taxonomic complexity of the genus make it a difficult one to deal with floristically. Many species are distinguished by small and subtle differences and, within certain groups, the systematics are poorly understood. In New England these difficulties are somewhat counter-balanced by the long history of collection and study of *Carex* by eminent caricologists beginning with Chester Dewey, Edward Tuckerman, and Francis Boott and continuing on into the 20th century with systematists such as M. L. Fernald. As an aside, the early studies of *Carex* in New England mean that many New England species, nearly 20% in fact, have their type locality in New England, thus adding to the desirability of protecting New England populations of these species.

While taxonomic problems can rarely be effectively solved by research confined to a local area, close study of a region can certainly lead to insights useful in studies over the entire range of a species. Also, since the particular combination of species in a region is usually unique, local areas may offer opportunities for studying the interactions of certain species.

This paper aims to outline known problem taxa in New England

Table 1. Recent research altering the status of New England *Carex* (excluding putative New England endemics).

| Treatment in Seymour (1982) | Revised Treatment | Reference |
|---|---|---|
| *C. convoluta* | *C. rosea* | Webber and Ball, 1984 |
| *C. rosea* | *C. radiata* | Webber and Ball, 1984 |
| *C. radiata* | *C. appalachica* | Webber and Ball, 1984 |
| *C. howei* | *C. atlantica* subsp. *capillacea* | Reznicek and Ball, 1980 |
| *C. incomperta* | *C. atlantica* subsp. *atlantica* | Reznicek and Ball, 1980 |
| *C. cephalantha* | *C. echinata* subsp. *echinata* | Reznicek and Ball, 1980 |
| *C. angustior* | *C. echinata* subsp. *echinata* | Reznicek and Ball, 1980 |
| *C. pensylvanica* var. *distans* | *C. lucorum* | Crins and Ball, 1983a |
| *C. crinita* var. *gynandra* | *C. gynandra* | Standley, 1983; Bruederle and Fairbrothers, 1986 |
| *C. walteriana* | *C. striata* | Reznicek and Catling, 1986 |

*Carex,* note ongoing work on the genus, and note relevant recently published work. As such, it provides an update to Seymour (1982). New England is quite well collected, and this paper hopefully will also focus attention of field botanists and students on problematic groups and stimulate thoughtful collecting in those areas where most good can be done. Putative New England endemics are briefly discussed, and a few overlooked aspects of biogeography relevant to conservation are noted.

## SYSTEMATIC PROBLEMS

Table 1 provides an update to Seymour (1982) for those native species of *Carex* for which detailed published treatments clarify New England species. Treatments which resulted neither in nomenclatural corrections nor taxonomic realignments at the species level are not included nor are minor nomenclatural adjustments such as changes in author citations. Unpublished theses also are not cited.

Table 2 attempts to outline taxonomic problems that have not yet been resolved in full, published treatments. If an abstract, thesis, or partial treatment is available, it is cited. The funda-

Table 2. Problematic *Carex* taxa without complete published revisions.

| Treatment in Seymour (1982) | Recent Alternative Treatments | Available Literature or Data Source |
|---|---|---|
| **1. Problems with circumscription of species** | | |
| *C. tincta*<br>*C. normalis* | *C. tincta* not recognized by Gleason and Cronquist (1963); suggested to be a hybrid | |
| *C. albolutescens* | *C. longii* segregated by Fernald (1950) | P. E. Rothrock (pers. comm.) |
| *C. brevior*<br>*C. molesta*<br>*C. merritt-fernaldii* | Only *C. brevior* recognized by Gleason and Cronquist (1963); *C. molesta* suggested to be a hybrid | J. M. Webber (pers. comm.) |
| *C. umbellata*<br>*C. abdita*<br>*C. tonsa* | Only *C. umbellata* recognized by Gleason and Cronquist (1963); nomenclature in doubt—cf. Mackenzie (1935) and Fernald (1950) | Rettig (1987) |
| *C. aurea*<br>*C. garberi* | Only *C. aurea* recognized by Boivin (1979) | P. W. Ball (pers. comm.), Katz et al. (1986) |
| *C. granularis* | *C. haleana* and *C. granularis* recognized by Mackenzie (1935) | |
| *C. katahdinensis*<br>*C. conoidea* | *C. katahdinensis* recognized only as forma by Boivin (1967) | R. Naczi (pers. comm.) |
| **2. Problems with ranks of taxa otherwise circumscribed similarly by authors** | | |
| *C. cephalophora*<br>*C. mesochorea* | *C. cephalophora* var. *mesochorea* (Gleason and Cronquist, 1963) | |
| *C. muhlenbergii* var. *muhlenbergii*<br>var. *enervis* | *C. muhlenbergii*<br>*C. plana* (Mackenzie, 1932) | |
| *C. cephaloidea*<br>*C. sparganioides* | *C. sparganioides* var. *cephaloidea* (Gleason and Cronquist, 1963) | |
| *C. annectens* var. *xanthocarpa* | *C. brachyglossa* (Mackenzie, 1932) | |

Table 2. Continued.

| Treatment in Seymour (1982) | Recent Alternative Treatments | Available Literature or Data Source |
|---|---|---|
| *C. tribuloides*<br>*C. projecta* | *C. tribuloides* var. *reducta* (Boivin, 1979) | J. M. Webber (pers. comm.) |
| *C. straminea*<br>*C. hormathodes* | *C. straminea* var. *invisa* (Gleason and Cronquist, 1963) | |
| *C. aenea*<br>*C. argyrantha* | *C. argyrantha* var. *aenea* (Boivin, 1979) | |
| *C. peckii*<br>*C. emmonsii*<br>*C. artitecta*<br>*C. nigromarginata* | *C. nigromarginata* with four varieties (Gleason and Cronquist, 1963) | Rettig (1987) |
| *C. lasiocarpa*<br>*C. lanuginosa* | *C. lasiocarpa* var. *latifolia* (Gleason and Cronquist, 1963) | |
| *C. debilis* | *C. debilis*<br>*C. flexuosa* (Mackenzie, 1935) | Waterway (1987a, 1987b) |
| *C. amphibola* | *C. grisea*<br>*C. amphibola* (Mackenzie, 1935) | R. Naczi (pers. comm.) |
| *C. tetanica*<br>*C. woodii* | *C. tetanica* var. *woodii* (Gleason and Cronquist, 1963) | |
| *C. albursina*<br>*C. laxiflora*<br>*C. striatula*<br>*C. blanda*<br>*C. gracilescens*<br>*C. ormostachya*<br>*C. leptonervia* | *C. laxiflora* with 6 varieties (Gleason and Cronquist, 1963); *C. leptonervia* also submerged as a variety by Boivin (1979) | Bryson (1980), Manhart (1986) |
| *C. flava*<br>*C. viridula* | *C. flava*<br>*C. cryptolepis*<br>*C. laxior* (Mackenzie, 1935) | Crins (1985), Crins and Ball (1983b, 1988) |
| *C. vesicaria* | *C. vesicaria*<br>*C. mainensis*<br>*C. raeana* (Mackenzie, 1935) | |

mental criterion for constructing this Table was disagreement about circumscription or rank of taxa among recent authors. A wide range of problems are thus included, from fundamental disagreements about distinctness and relationship to minor philosophical quibbles about rank of taxa otherwise circumscribed identically. A large number of varietal names are attributed to species of New England *Carex.* In some cases, these have proven to be significant and are here considered. In the majority of cases, these are simply subdivisions of continuous variation with little or no geographic segregation and are not included. Again, minor nomenclatural disagreements are not included, nor are difficult complexes with only one species in New England, or hybrids, unless these have been treated as species by some authors.

The information in Table 2 can be readily gleaned from the literature. However, presentation of it all together illustrates powerfully the substantial degree of disagreement and the magnitude of work left to be done. Of course, the fact that it is possible to draw up such a list as Table 2 is really a testimony to how well known the flora is. At least the problem areas are known! Naturally, this table is also not necessarily complete. One cannot easily anticipate problems such as unrecognized cryptic species nor precisely predict range extensions of members of problem groups into New England.

Fully 46 species, about 25%, of New England *Carex* are involved in taxonomic disagreements among recent authors, a somewhat startling statistic considering that the New England flora is traditionally considered to be well understood. Of course, many of these disagreements are minor, and thorough revision may not result in substantial changes to the taxonomic status of many species.

## NEW ENGLAND ENDEMICS

Three species of *Carex* have been generally considered to be endemic to New England: *C. elachycarpa, C. josselynii,* and *C. oronensis.* The first two species were studied by Reznicek and Ball (1979). *Carex elachycarpa* was demonstrated merely to be a variant of the eastern North American calciphile *C. sterilis. Carex josselynii* was more of a puzzle, but was referred, with some hesitation, to *C. echinata.* The recent discovery of plants with morphology similar to *C. josselynii* in the St. John River system

in adjacent New Brunswick (Hinds, 1986) has prompted continued recognition of the plant as a species. More work is needed here.

*Carex oronensis* Fern. in sect. *Ovales* is still an unsolved puzzle, but work by Allison Dibble (pers. comm., 1988) should soon resolve the problem.

## PHYTOGEOGRAPHICAL CONSIDERATIONS

A detailed phytogeographic analysis of such a large group of plants as New England *Carex* is beyond the scope of this brief article. Indeed, it could be the subject of a large paper on its own (Raymond, 1951). A few aspects where phytogeography may directly impinge on conservation of and research on rare species are, however, here noted.

Knowing plant distributions and habitats, both within New England and in adjoining areas, greatly aids in discovering the precise status of rare species in each state. It can even point to probable additions as yet undiscovered, such as the northwestern *Carex sychnocephala* which occurs in Quebec very close to Vermont (Rousseau, 1974), and the boreal *C. concinna* and *C. rostrata sensu stricto* (Reznicek, 1985) which occur close to the Maine border in New Brunswick (Hinds, 1986). A number of New England's rarer *Carex* are western or northwestern calciphiles, including such species as *C. sterilis, C. richardsonii, C. atherodes,* and *C. molesta,* and knowledge of their distribution and ecology can help pinpoint occurrences of rare habitats.

As implied in the previous paragraph, rare species in a given area are quite frequently species at the edges of their ranges. Biologically it may not make sense to be concerned about a species in a particular area if it is common in adjacent regions. This overlooks both the need to work within political boundaries due to legislation and the obligation of each state to protect its own natural heritage. In addition, marginal populations of species are frequently somewhat genetically differentiated.

There may also be some relevance to whether or not a species is northern or southern in distribution with respect to New England. With minor fluctuations, vegetational changes in New England after de-glaciation have primarily involved gradual displacement to the north and to higher elevations of boreal and arctic-alpine species by deciduous forest species from the south.

Northern species now mostly persist as more or less disjunct occurrences in small pockets of cooler habitats, including such sites as springy seeps, alpine areas, conifer swamps, cliffs and exposed headlands, deep ravines, shores of large lakes and rivers, etc. Although there are exceptions, many southern species, by contrast, now have ranges that stop relatively abruptly, with fewer isolated, disjunct occurrences. This trend can be relatively easily detected by comparing distributions of northern and southern species in a mapped flora such as that for Michigan (Voss, 1972, 1985).

The practical consequence of this is that if a northern species is lost from a site, not only is there likely not to be a nearby site producing propagules for recolonization, but suitable habitat is restricted to tiny pockets. Many rare southern species may have occurrences relatively nearby from which recolonization may occur if a species is lost from a site—even if the occurrences are on the other side of the state line. Available habitat is also not necessarily restricted to tiny pockets.

This point is of particular relevance to *Carex,* since the genus is so important in arctic-alpine and boreal regions. About 13% of New England *Carex* are boreal or arctic-alpine, including such restricted species as *C. capitata, C. capillaris, C. livida, C. media, C. saxatilis, C. rariflora,* and *C. vaginata.* However, northern species of *Carex* are disproportionately represented in rare plant lists for New England, constituting nearly 40% of the species in the list compiled by Crow et al. (1981). And, based on the considerations noted above, I would also predict that relatively fewer new stations and major range extensions will be found in the future for northern species as contrasted with southern species.

## CONCLUSIONS

Considering how well known the systematics of New England plants is generally thought to be, a surprising 25% of the *Carex* are involved in taxonomic controversy. More research is clearly needed, but resolution of these problem areas does require revisionary work beyond the boundaries of New England, so as to include the entire ranges of the species or species complexes. Dealing in the meantime with unrevised groups obviously presents a problem. Fortunately, only a minority of problem groups include rare species. Primarily for the sake of information gath-

ering, it is probably best to be a "splitter" until evidence to the contrary is convincing. It is easy to join two sets of data into one, but it may be impossible to split data. This approach may lessen the upheavals in rare plant treatments that might otherwise happen when the taxonomy of a group is resolved.

Just as knowing a species' biology is the key to protecting it, so knowing accurately species systematics, geographical distribution, and abundance is the key to knowing what to protect. While solving systematic problems will take time, study of the regional distribution and abundance of species is both feasible in the short term and worthwhile. When a real effort has been made to study plants in the field, it is surprising how often information gleaned from herbaria has been misleading or wholly unrepresentative.

Some biogeographical factors, such as disjunctions of stations, the overall abundance and range of species and whether or not the species is endemic are taken into account routinely in conservation of rare species. An additional factor to be considered is whether or not the species is of southern or northern affinity with respect to a particular area, northern species being potentially more threatened.

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RHODORA, Vol. 91, No. 865, p. 153, 1989

# A DEMOGRAPHIC MODEL FOR *PEDICULARIS FURBISHIAE*, WITH IMPLICATIONS FOR CONSERVATION STRATEGIES

SUSAN C. GAWLER

ABSTRACT

Four years of demographic data on over 5000 individuals of *Pedicularis furbishiae* provided size-specific survivorship and fecundity estimates used to model the population dynamics of this endangered plant. Survivorship and fecundity varied not only with size, but also with the population's environment, particularly the soil moisture level and time since disturbance of its riparian habitat. The model used to investigate population dynamics incorporated these effects, and added stochastic disturbance-caused mortality. Under observed frequencies and intensities of disturbance, the model predicted that few populations would remain extant for more than 30 years and that populations on drier sites would be even shorter-lived. Conservation of *P. furbishiae* thus relies on maintenance of stretches of suitable habitat for the establishment of new colonies. A protection approach limited to currently extant colonies would be unlikely to succeed.

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# NOTES ON PROPAGATION OF RARE NEW ENGLAND SPECIES

WILLIAM E. BRUMBACK

## ABSTRACT

Propagation and cultivation of endangered species can provide information on species biology, provide reserve collections in the event of catastrophe in the wild, educate the public at botanical institutions, and provide plants for reintroduction or introduction to the wild. Propagation notes on New England rare species include *Eupatorium leucolepis* var. *novae-angliae, Trollius laxus, Oxytropis campestris* var. *johannensis, Schwalbea americana, Agalinis acuta, Astragalis robbinsii* var. *jesupi, Polemonium van-bruntiae, Mimulus ringens* var. *colpolphilus,* and *Scirpus longii.*

Key Words: *Eupatorium leucolepis* var. *novae-angliae, Trollius laxus, Oxytropis campestris* var. *johannensis, Schwalbea americana, Agalinis acuta, Astragalis robbinsii* var. *jesupi, Polemonium van-bruntiae, Mimulus ringens* var. *colpolphilus, Scirpus longii,* propagation, endangered species, New England

## INTRODUCTION

Since the publication of lists of rare and endangered species for each of the New England states (Church and Champlin, 1978; Coddington and Field, 1978; Countryman, 1978; Eastman, 1978; Mehrhoff, 1978; Storks and Crow, 1978) and for New England as a region (Crow et al., 1981) there has been increased interest in the cultivation and propagation of endangered plants. Rare plant propagation is useful for several reasons:

1. Propagation research can provide important information on species biology. Although not all *ex-situ* research may be directly applicable to wild populations, most physiological characteristics of plants in cultivation are the same as far as we know (Raven, 1979). Furthermore, if propagation material is taken directly from wild populations, the research may provide immediate information on the behavior of the species in the wild. However, more often than not, this research will raise more questions about the behavior of wild populations. For example, if seed collected from a wild population germinates with relative ease in cultivation, and there is a scarcity of young plants in the wild, researchers may wish to focus on seedling establishment in field research.
2. Propagation provides reserve collections in the event of catastrophe in the wild. These collections are likely to be genetically

different from the wild populations for a variety of reasons (Brumback, 1981), but they nevertheless provide material as a reserve if wild populations are destroyed. There are a number of species now in cultivation that no longer exist in the wild, including *Franklinia alatamaha* (Ayensu and DeFilipps, 1978).

The recent initiation of seed banks and reserve collections at botanic gardens throughout the U.S. through the Center for Plant Conservation (CPC) (Jamaica Plain, MA) is part of a plan to provide that all the endangered plants of a region be part of a national reserve collection. These reserve collections can also provide research material to other researchers so that the need to further collect from already dwindling wild populations is obviated.

3. Rare plant propagation provides specimens to botanical gardens and universities so that the public will become aware of the beauty of (and the issues surrounding) our endangered species. Furthermore, these display collections can relieve pressure on wild populations by providing viewing sites for plants whose wild populations might be damaged by repeated visits by plant enthusiasts.

4. Propagation provides plants for introduction or re-introduction should this action be deemed advisable by wildlife managers. Successful reintroduction has already been achieved in a number of areas including Oregon (CPC, 1987, 1988). It appears inevitable that the current pace of development will necessitate more reintroduction of rare plants.

Propagation and cultivation of some plant groups, especially terrestrial orchids and semi-parasites of the Scrophulariaceae, is notoriously difficult. However, many other species, when removed from competition in the wild, thrive in cultivation. In propagating any endangered plant, it is advisable to discuss methods with horticulturists from other parts of the country. It may be that the species is not rare in another area and propagation information is sometimes available.

The general approach used in cultivating and propagating plants at the Garden in the Woods (GITW), the botanical garden of the New England Wild Flower Society, has been to attempt to match the natural conditions found in the wild, and when possible, to allow natural processes (i.e., winter freezing and thawing) to stimulate germination of seed.

When dealing with wild-collected rare plant seeds, it is important that collection from the wild should not adversely affect the population in any way. Therefore, only small numbers of seeds of rare plants are usually available for germination testing, and thus, these tests may not contain a statistically valid number of seeds. For the same reason, replication of trials is often not possible.

## METHODS

Unless otherwise noted, the following methods were used. Seeds were sown on a moistened mix of Rediearth (commercially available peat-lite germination medium), peat moss, and coarse concrete sand in Pen Packs (plastic containers 6 × 3 × 5 inches). After sowing, seeds were either covered lightly with sand or allowed to remain uncovered in full light. All seeds not covered had glass or plastic placed on top of the flat in order to conserve moisture until germination was complete. In order to avoid disturbing seeds as they germinated, flats without sand covering were watered from below by immersing the flat ½ of its depth in water until the surface was moist. Flats that were covered with sand after sowing were watered gently from above. After sowing, flats were moistened and either 1) placed outside under natural conditions, 2) remained in the Solar Greenhouse (SGH) at a minimum night temperature of 55°F, or 3) were enclosed in a plastic bag and placed in a refrigerator for several months at 35–40°F.

Softwood cuttings were taken from the tips of stems and were approximately 1–2 inches long. The cuttings were moistened, the ends were dipped in Hormoroot A (active rooting hormone .01% indolebutyric acid), and stuck in coarse concrete sand under intermittent mist (Geiger Mist-a-matic) without bottom heat. Temperatures in the solar greenhouse after June 1 are at least 80°F during the day.

The mixtures used to pot seedlings or cuttings varied with the species, but basically all mixtures made use of our regular potting soil combined with sand to increase drainage and peat moss to increase acidity where appropriate. Our regular soil consists of a combination of compost, peat moss, perlite, sand, and dehydrated cow manure to produce a mixture that retains moisture, yet is well-drained. Containers held outside over winter are covered with ¼-inch Microfoam (a commercially-available thermal blan-

ket) and white polyethylene plastic. The containers freeze over winter, but roots and buds are not normally damaged. The protection mitigates heaving of small plants or seeds due to freezing and thawing.

## NOTES ON NEW ENGLAND RARE SPECIES

The following species, with the exception of *Polemonium vanbruntiae,* were listed as Threatened and Endangered Plant Species Considered for Federal Listing which occur in New England in Crow et al. (1981).

*Eupatorium leucolepis* (DC.) T. & G. var. *novae-angliae* Fern.

Softwood cuttings taken in summer rooted easily. Seeds collected from the wild on Sept. 12, 1984 (Prop. #84p-554) and sown onto a flat outside germinated in May, 1985. Seed collected from plants growing at the Garden in the Woods on Oct. 5 and 7, 1985 was dried at room temperature and stored under refrigeration (38°F) until sowing April 4, 1985 (Prop. #85p-247). Seed was divided into two groups. Group A was placed outside immediately after sowing and Group B was enclosed in a plastic bag and placed in a refrigerator until June 28, 1985 when the flat was placed outside. Group A germinated in May, 1985 approximately 1 month after sowing. Group B germinated on July 14, 1985. By September, 1985 both groups of seedlings had grown significantly and were in bloom in the seed flats.

This species appears easy to propagate from both seeds and cuttings. Seed germination may be slightly better if seeds are given a pretreatment of cold (either dry or moist cold), but as in many members of the Asteraceae (Young and Young, 1986), seed will germinate without pretreatment.

*Trollius laxus* Salisb.

This species has been present at the Garden in the Woods (GITW) since 1940 and seed germination has been traditionally strong. Seed sown outside one month after collection (late May and early June) from the population at GITW did not germinate until the following spring (30% germination—50 seeds sown). Seed sown at the same time into a seed flat and placed in a

refrigerator for three months germinated within two weeks after being removed from the refrigerator and placed in the SGH. Seed from this same collection that had been stored dry in a refrigerator for nine months failed to germinate when sown outside in March. However, this flat remained outside for the summer and was given protection overwinter in a cold frame. Germination of this seed was near 100% in the spring. In repeated collections for commercial production of this species at GITW, seed collected in early June, allowed to dry at room temperature for several months, then stored dry in a refrigerator until sowing outside in November has germinated well each spring.

This species is relatively easy to grow from seed. Parsons and Yates (1984) have shown that seedlings grow better in calcareous soil than in acid soil and seed benefits from a warm, moist period before being subjected to a cold, moist period. Although this warm, moist period does not appear always necessary to successful production of *Trollius laxus* in our tests, sowing the seed immediately after ripening and allowing the seeds to achieve a warm, moist period after ripening outside over summer may produce better germination. A period of moist cold is necessary in any event. Seed sown in fall typically produces blooming size plants during the second growing season after germination.

*Oxytropis campestris* DC. var. *johannensis* Fern.

Seed collected August 6, 1986 in the wild and sown two days later (50 seeds—Prop. #86p-538) resulted in 3 seedlings within 3 weeks of sowing. At the same time, seed was sown onto a flat and placed in a refrigerator for 3 months of moist cold. Upon returning to a warm greenhouse, 6 seedlings had germinated by May of 1987. Seed from the same collection in August of 1986 was allowed to dry and was stored in a refrigerator from one week after collection until sowing on April 7, 1987. Seed was divided into two groups of 50 seeds (Prop. #87p-421). Group A, sown outside, germinated within 3 weeks of sowing and resulted in 13 seedlings. Group B, sown and placed in the refrigerator for 2 months before being placed outside, germinated very strongly, but no exact number was counted. Likewise, seed held dry in a refrigerator from one week after collection, and sowed outside Nov. 12, 1987 germinated very strongly in spring 1988 (no count of seedlings made).

It is apparent that seed of this species will germinate without

a period of moist cold, but dry, cool storage of seed followed by moist refrigeration or outdoor temperatures through winter may give better germination. This plant is reputedly short-lived in cultivation (Dr. George Newman, Bedford, NH, pers. comm.). The plants bloomed in cultivation during the second year of growth following germination.

*Schwalbea americana* L.

Seed collected in November in the wild (Prop. #82p-478) sown immediately in a warm greenhouse (SGH) germinated slightly by January. However, seed sown outside at the same time and allowed to remain outside all winter produced far better germination in the spring. Seed that was not covered with sand after sowing had obviously better germination in both instances. Repeated attempts at germination since this 1982 test have resulted in either no germination or only one or two seedlings. All seedlings have eventually died. This species is a member of the Scrophulariaceae, and appears to be semi-parasitic, at least in the seedling stage. Other growers have reported (George Newman, Bedford, NH, pers. comm.) that seeds germinated, but that all seedlings eventually die.

Musselman and Mann (1978) grew this species from seed by sowing seed directly into pots containing 1-year-old tree species. They reported haustoria (root attachment) to 16 of 19 tree species tested. It appears that many semi-parasites form haustoria on widely varied hosts, and thus may not be host-specific. Experiments are underway to test the germination and growth of *Schwalbea* when sown with various native grass species.

*Agalinis acuta* Pennell

Seed received in October, 1983 (Prop. #83p-519) and sown under grow lights (no sand cover) germinated without cold treatment. Other seed sown outside in November, 1983 germinated in spring 1984 and bloomed slightly by September, 1984. However, the seedlings were depauperate, blooming at only 3 inches in height. Since this species is an annual, the seedlings died shortly after bloom.

In our trials, this species germinated as would a typical annual, but growth was never strong after germination. Further testing

should provide more information on whether this member of the Scrophulariaceae also needs a host plant for proper growth despite the fact that it is an annual.

*Astragalus robbinsii* (Oakes) Gray var. *jesupi* Egglest.

Germination from seed collected in July was very poor when sown immediately after collection. A three-month period of moist cold on this same trial did not increase seed germination significantly. However, seed stored in dry cold in the refrigerator and sown outside in November resulted in over 50% germination the following spring (46 seeds sown). Mortality of these seedlings was high, probably due to improper drainage in the soil mix after the seedlings were potted.

It is likely that this species, like many Leguminosae (Young and Young, 1986) has a hard seed coat and that the freezing and thawing over winter enable the seed to take up water and germinate in the spring. It is possible that overnight soaking in water or scarification followed by moist, cold refrigeration would give good results. The problems of mortality of plants after germination can probably be overcome by treating the plants to a more well-drained soil mixture.

*Polemonium van-bruntiae* Britt.

Seed of this species did not germinate well immediately after collection from the wild in August, 1986, either with or without a period of moist cold (Prop. #86p-786 and 86p-548). However, the same seed when held dry under refrigeration from September, 1986 until sowing outside in April, 1987 germinated very well. In other tests with this same seed, germination has been erratic, but seed held dry under refrigeration until sowing outside in November, 1987 germinated extremely well.

Although other species of *Polemonium,* including *caeruleum,* have typically germinated at GITW without cold treatment, this variety does seem to germinate better after a period of moist cold. However, results in several trials have been erratic. This variety bloomed during its second year of growth.

*Mimulus ringens* L. var. *colpophilus* Fern.

Seed of this species needs no pretreatment for germination, but germination may be better if the tiny seed is not covered with

sand or other medium after sowing. It is not clear whether this variety is taxonomically valid, and tests are underway to establish if *ringens* var. *ringens* and *ringens* var. *colpophilus* show the differing growth habits that appear in the wild when grown together under identical conditions in cultivation. Plants bloomed during their second growing season.

*Scirpus longii* Fern.

Seed collected in June, 1987 and sown within two weeks of collection (no covering on top of the seed after sowing) germinated 34% within 3 months (50 seeds sown). The same seed given a cold treatment did not germinate as well. The seedlings quickly grow to a robust size and container growing has been very successfully to this point.

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# THE 1988 JESSE M. GREENMAN AWARD

The 1988 Jesse M. Greenman Award has been won by John H. Wiersema for his publication "A Monograph of *Nymphaea* Subgenus *Hydrocallis* (Nymphaeaceae)," which appeared in *Systematic Botany Monographs,* volume 16. This monograph is derived from a Ph.D. dissertation submitted to the University of Alabama, under the direction of Dr. Robert R. Haynes. Dr. Wiersema based his classification on numerical taxonomy, scanning electron microscopy of seeds and pollen, chromosome numbers, floral biology, artificial hybridization, flavonoid chemistry, and general morphology. Fourteen species are recognized in the subgenus, which is restricted to the American tropics and subtropics, and one new subspecies is proposed.

This Award is named for Jesse More Greenman (1867–1951), who was Curator of the Missouri Botanical Garden Herbarium from 1919 until 1943. A cash prize of $250 is presented each year by the Garden, recognizing the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation that was published during the previous year.

Nominations for papers published during 1988 are now being accepted for the 21st annual award, which will be presented in the summer of 1989. Reprints of such papers should be sent to:

Greenman Award Committee
Research Division
Missouri Botanical Garden
P.O. Box 299
St. Louis, MO 63166-0299, U.S.A.

In order to be considered for the 1989 award, reprints must be received by June 1, 1989.

# NEBC AWARD
# FOR THE SUPPORT OF BOTANICAL RESEARCH

The New England Botanical Club will again offer an award of $1000 in support of botanical research to be conducted in relation to the New England flora during 1989. This award is made to stimulate and encourage botanical research on the New England flora and to make possible visits to the New England region by those who would not otherwise be able to do so. The award will be given to the graduate student submitting the best research proposal dealing with field studies in systematic botany, biosystematics, and plant ecology, but proposals for research in other areas of botany will also be considered. This award is not limited to graduate students at New England institutions, nor to members of the New England Botanical Club. Papers based on this research must acknowledge the NEBC's support, and it is encouraged that they be submitted to *Rhodora,* the Club's journal, for possible publication—subject to standard review processes.

Applicants should submit a proposal of no more than three double-spaced pages, a budget (the budget will not affect the amount of the award), and a curriculum vitae. Two letters, one from the student's major professor, in support of the proposed research are also required. Proposals and supporting letters should be sent before 28 February 1989 to:

Awards Committee
The New England Botanical Club
22 Divinity Avenue
Cambridge, MA 02138

The recipient of the award will be notified by 30 April 1989.

# MEETING ANNOUNCEMENT AND CALL FOR ABSTRACTS NEW ENGLAND BOTANY GRADUATE STUDENTS

The fourth New England Botany Graduate Student Meeting will be hosted by the Department of Botany and the Pringle Herbarium at the University of Vermont, Burlington, VT on Saturday April 15, 1989. Attendance is open to all. Paper presentations will be largely restricted to graduate student research (completed or in progress) representing all areas of botany (systematics, ecology, reproductive biology, anatomy, physiology, etc.). Time slots for paper presentations are limited and prior registration is required. Abstracts are due by Wednesday, March 15, 1989.

For information and abstract forms, contact Cathy Paris or Alison Dibble, organizers.

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# THE NEW ENGLAND BOTANICAL CLUB
22 Divinity Avenue
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The New England Botanical Club is a non-profit organization that promotes the study of plants of North America, especially the flora of New England and adjacent areas. The Club holds regular meetings, has a large herbarium of New England plants, and a library. It publishes a quarterly journal, RHODORA, which is now in its 90th year and contains about 500 pages a volume.

Membership is open to all persons interested in systematics and field botany. Annual dues are $25.00, including a subscription to RHODORA. Students may apply for a Student Membership at $10.00 a year, which does not include a subscription to RHODORA. Members living within about 200 miles of Boston receive notices of the Club meetings.

To join, please fill out this membership application and send with enclosed dues to the above address.

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| Regular Member | $25.00 |
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*Vol. 90, No. 864, including pages 355–486, was issued October 31, 1988.*

# INFORMATION FOR CONTRIBUTORS TO RHODORA

Submission of a manuscript implies it is not being considered for publication simultaneously elsewhere, either in whole or in part.

Manuscripts should be submitted in **triplicate** (an original and two xerographic copies) and *must be double-spaced* (at least 3/8") **throughout** including tables, figure legends, and literature citations. The list of legends for figures and maps should be provided on a separate page. Footnotes should be used sparingly. Do not indicate the style of type through the use of capitals or underscoring, particularly in the citation of specimens. Names of genera and species may be underlined to indicate italics in discussions. Specimen citations should be selected critically, especially for common species of broad distribution. Systematic revisions and similar papers should be prepared in the format of "A Monograph of the Genus *Malvastrum*," S. R. Hill, Rhodora 84:1–83, 159–264, 317–409, 1982, particularly with reference to indentation of keys and synonyms. Designation of a new taxon should carry a **Latin diagnosis** (rather than a full Latin description), which sets forth succinctly just how the new taxon is distinguished from its congeners. Papers of a floristic nature should follow, as far as possible, the format of "Annotated List of the Ferns and Fern Allies of Arkansas," W. Carl Taylor and Delzie Demaree, Rhodora 81: 503–548, 1979. For bibliographic citations, refer to the Botanico-Periodicum-Huntianum (B-P-H, 1968) which provides standardized abbreviations for journals originating before 1966. All abbreviations in the text should be followed by a period, except those for standard units of measure and direction (compass points). For standard abbreviations and for guidance in other matters of biological writing style, consult the *CBE Style Manual,* 5th ed. (original title: *Style Manual for Biological Journals*). In preparing figures (maps, charts, drawings, photos, etc.) please remember that the printed plate will be 4 × 6 inches; be sure that illustrations are proportioned to reduce correctly, and indicate by blue pencil the intended limits of the figures. (Some "turn-page" figures with brief legends will be 3½ × 6 in.) Magnification/reduction values given in text or figure legends should be calculated to reflect the actual printed size. An Abstract and a list of Key Words should be supplied at the beginning of each paper submitted, except for a very short article or note. All pages should be numbered in the upper right-hand corner. Brevity is urged for all submissions.

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# Rhodora

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# RHODORA



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*Agalinis acuta* Pennell (Sand-Plain Gerardia). A very rare plant of the coastal plain in danger of extinction; known only from Cape Cod and Long Island. Recently listed by the U.S. Fish & Wildlife as Threatened. Original artwork by Tess Feltes; from *New England's Rare, Threatened and Endangered Plants.* Crow, G. E. 1982. Reproduced by permission.

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# THE TYPE SPECIES OF THE GENUS *SABATIA* ADANSON (GENTIANACEAE)

ROBERT L. WILBUR

## ABSTRACT

The type species of the genus *Sabatia* Adans. (Gentianaceae) is *S. dodecandra* (L.) BSP. and not the species so designated in *Index Nominum Genericorum*. The status of the genera proposed by Adanson in *Familles des Plantes* is briefly discussed and it is suggested that stability would be better served by accepting *Familles des Plantes* by Adanson as a valid source of generic names rather than to discard it as has been recently recommended.

Key Words: *Sabatia, Gentiana,* typification, Gentianaceae, North America

The gentianaceous genus *Sabatia* consists of approximately twenty species primarily of the eastern United States but ranging to a limited extent into eastern Canada, the West Indies, and Mexico. Until recently the type species of *Sabatia* Adans. had invariably been stated to be *S. dodecandra* (L.) BSP. (Britton and Brown, 1913; Blake, 1915; Wilbur, 1955; Perry, 1971; Wood and Weaver, 1982). This generic typification had generally been unchallenged and alternative nominees to be the type species of *Sabatia* Adans. have not been suggested to my knowledge before the unfortunate entry in *Index Nominum Genericorum* (= ING) (1979, 3: 1541) where the type of *Sabatia* is indicated to be *Gentiana saponaria* L.

*Sabatia* was originally published by the highly individualistic Adanson in his *Familles des Plantes* 2: 503. 1763 as an apparently monotypic genus and as such, in Adanson's nomenclatural system, it bore only the generic name without a specific epithet. The various genera were contrasted briefly in a tabular chart and for *Sabatia* we learn that it was based on "Gentiana Gronov. virg. 29," a reference to p. 29 of *Flora Virginica* published by Gro-



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novius based on a manuscript sent by John Clayton where very adequate diagnoses appear. Three species of *Gentiana* were described on p. 29 of *Flora Virginica*. Only one of these three species was there described as having the sepals, petals, and stamens each in twelves as indicated by Adanson in his tabular chart as features of his newly described genus *Sabatia*. The Gronovian polynomial for this species, which often does have a 12-parted flower, is *Gentiana floribus duodecim petalis, foliis distinctis*. Linnaeus (Sp. Pl. 1: 190. 1753) based his *Chironia dodecandra* solely upon this Gronovian polynomial, although he mistakenly and carelessly cited "Gron. virg. 27," a page dealing exclusively with asclepiads and which of course does not bear the Gronovian polynomial quoted by Linnaeus.

There seems no reason whatsoever to consider two of the three species named as species of *Gentiana* on Gronovius' *Flora Virginica* p. 29 as the type of *Sabatia* Adans.: 1) *Gentiana caule ramisque ramosissimus, foliis subulatis minimis* has 5 sepals and 5 yellow petals, excluding it obviously from consideration as a possible type of the 12-parted *Sabatia* Adans.; it was given the binomial *Sarothra gentianoides* L. (Sp. Pl. 1: 272. 1753) and is usually known to us as *Hypericum gentianoides* (L.) BSP.; and 2) *Gentiana floribus ventricosis campanulatis erectis quinquefidis, foliis ovato-lanceolatis,* which Linnaeus cited as *Gentiana saponaria* (Sp. Pl. 1: 228. 1753), is a compound Linnaean species from which *G. catesbaei* Walt. has since been segregated. Clearly *Gentiana saponaria* L. has no claim to be considered the type of *Sabatia* Adans. in spite of its listing in ING. The 5-parted calyx and corolla and the 5 anthers of *Gentiana saponaria* all conflict with the stated 12-parted calyx and corolla and the twelve laterally twisted anthers indicated as the diagnostic features by Adanson for his *Sabatia*. The type of the genus *Sabatia* Adans., therefore, remains the species known as *Sabatia dodecandra* (L.) BSP.; it has nothing to do with *Gentiana saponaria,* the species wrongly stated to be its type in the invaluable and usually most reliable reference *Index Nominum Genericorum*.

The above might all be left unsaid as so obviously a careless error that it would be apparent to all or at least to all living within the range of the genus and even remotely concerned with it. However, Parkinson (1987a, 1987b, 1987c, 1987d) has published a series of papers challenging the legitimacy of all the generic names published in Adanson's *Familles des Plantes* and in it repeated

the ING error concerning the typification of *Sabatia.* Parkinson argues that Adanson clearly did not accept or utilize the Linnaean binomial system and consequently all of Adanson's many generic proposals lack legitimacy. To be used in the future these names, in Parkinson's opinion, must either be conserved or if taken up by a later author, the generic name is to be attributed to that later author as the publishing author and not to Adanson. It seems most unlikely that Adanson's *Familles des Plantes,* a work that has been considered as a legitimate source of many generic names by most investigators for over a century, will be ruled as an invalid source based on Parkinson's conclusion that Adanson's failure to provide a binomial for either the first (= type) species of the genus or of a monotypic genus constitutes adoption of unitary nomenclature. In Parkinson's opinion this failure rendered all the names in the book invalidly published as being contrary to Art. 20.4b of the ICBN. It would seem to me that Adanson was reasonably within the Linnaean binomial system but chose this idiosyncratic method of denominating the original or typical element of the genus. Convention plays a role in such matters, and it has been botanical convention for more than a century to accept Adanson's *Familles des Plantes* as a valid source of generic names. Parkinson recognized as much (1986a, p. 95) and predicted that many will want to modify the code so that Adanson's genera may continue to be accepted as they have been in the past. After all, generic names are accepted from John Hill's *The British Herbal* (1756–57) and other post-1753 botanical works which did not approximate the Linnaean binomial system nearly as closely as did Adanson's publication.

It should be pointed out that Parkinson's analysis of the minor adjustments required by his suggested mandatory abandonment of Adanson's *Familles des Plantes* as a source of validly published generic names seems overly optimistic. The numerous changes required if *Familles des Plantes* were to be proscribed would, in my opinion, be much more drastic than advertised. If, as suggested by Parkinson, we were to accept the generic name of this gentianaceous genus as starting with Salisbury (1806) we find that the generic name in *Paradisus Londinensis* appeared as *Sabbatia* and not *Sabatia.* The lengthy effort to get botanists to follow Adanson's original orthography of *Sabatia* as required by Art. 73 of the ICBN would then need to be reversed; *Sabbatia* Salisb. (Parad. Lond. 1806) might then be the correct generic name and

orthography except that *Sabbatia* Moench (Meth. 386. 1794) clearly has priority over Salisbury's publication. Furthermore, *Sabbatia* Moench is an earlier name for the large mint genus *Micromeria* Benth. (Edward's Bot. Reg. 15: sub *t. 1282.* 1829) which is currently conserved but would need to be reconserved if Adanson's generic names from *Familles des Plantes* were to be now ruled as illegitimate. Salisbury described and illustrated an annual species that spontaneously appeared in his London garden that he took to be the same as *Chironia gracilis* Michx. However, the species Salisbury described and illustrated was the plant that has been called *Sabatia stellaris* Pursh, an annual usually of saline flats, while *Chironia gracilis* Michx. is a perennial of definitely non-saline savannahs, swales, and open piney woods. Prior to the Sydney Botanical Congress (1981), this problem of typification would have been settled in favor of the species described (i.e., *S. stellaris* Pursh, a species formally named by Pursh in 1814). Since the Sydney Botanical Congress, Article 10.1 of the 1983 ICBN mandates that the type be determined by the species named and not by the species described. The type of the genus *Sabbatia* Salisb. would then be *S. gracilis* (Michx.) Salisb. (= *S. campanulata* (L.) Torr.), a species belonging to a very different section of the genus than *S. dodecandra* (L.) BSP., the usually recognized type of the genus *Sabatia* Adans. It does not require the vision of an astrologer to predict that the adjustments required by the acceptance of Parkinson's argument for the non-legitimacy of the generic names proposed by Adanson would be considerably more drastic than suggested. It would seem to me not to be in the interest of nomenclatural stability to rule at this late date that all generic names in Adanson's *Familles des Plantes* were invalidly published.

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# MORPHOLOGICAL VARIATION IN SOUTHERN APPALACHIAN *BETULA ALLEGHANIENSIS* AND *B. LENTA* (BETULACEAE)

JERI WELSH HIGGINBOTHAM,[1] MARILOU CURTIS, AND CLIFFORD R. PARKS

## ABSTRACT

Variation in leaf, fruit, bract, and catkin morphology of *Betula alleghaniensis* Britt. and *B. lenta* L. was studied along the elevational gradient in the southern Appalachians in order to characterize the regional structure of the two species. Populations at 52 sites were sampled in North Carolina and adjacent parts of Tennessee, Georgia, and South Carolina. Weak to moderate linear relationships with elevation were found in most size attributes for both species. A few shape characters were also correlated with elevation for one or the other species. *Betula alleghaniensis* was significantly more variable than *B. lenta* for 28 of the 44 characters analyzed. Levels of variability in both species approximated or exceeded levels found in other regions. Low-elevation rather than high-elevation southern Appalachian *B. alleghaniensis* appears to be more similar to the northern form. However, due to the nature of the morphological cline, the authors found no validity to varietal distinctions in yellow birch.

Key Words: *Betula,* birch, cline, morphology, phenotypic variation, southern Appalachians

## INTRODUCTION

Both *Betula alleghaniensis* Britt. (yellow birch) and *B. lenta* L. (sweet, black, or cherry birch) belong to Winkler's (1904) subsection *Costatae* Regel of Section *Eubetula* Regel. This subsection, with its center of diversity in northeastern Asia, includes only four taxa native to North America: *B. alleghaniensis, B. lenta, B. nigra* L. (river birch), and *B. uber* (Ashe) Fern. (round-leaf birch). Morphological, chemical, and hybridization data indicate a close affinity between yellow and sweet birch. The rare round-leaf birch is thought to be allied to sweet birch (Sharik and Ford, 1984). River birch is considered distantly related to sweet and yellow birch (Clausen, 1973).

Both yellow and sweet birch are important, widespread hardwood components of the Appalachian forests. Sweet birch is found from Maine south to the mountains of Alabama and Georgia

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(Little, 1971). Yellow birch ranges from Ontario east to Nova Scotia and south to the mountains of Georgia and South Carolina (Little, 1971; Clausen, 1973).

The elevational amplitude of both species is greatest in the southern Appalachians. Here, yellow birch ranges in elevation from 300 m to 1900 m, and sweet birch from 300 m to 1550 m. The two occur together at mid-elevations (600 m to 1400 m) in association with other components of the mixed mesophytic forest. In this area of sympatry, yellow birch and sweet birch occur intermixed on moister slopes. On drier slopes, yellow birch grows most often along streamsides; sweet birch is typically found further upslope.

Morphological variation in both taxa, particularly in yellow birch, has been the source of some confusion over the years, as evidenced by the nomenclature which has entered into the literature and its subsequent application. Britton (1904) wrote of his newly segregated yellow birch, *Betula alleghaniensis,* that it resembled both *B. lutea* Michx. f. (then the standard name for yellow birch; now a synonym of *B. alleghaniensis*) and *B. lenta,* though it was smaller than *B. lutea.* Britton further described his new taxon as having bark "either close and furrowed, or peeling off in thin yellowish-gray layers," and leaves "mostly cordate at the base but sometimes rounded." The type specimen for this new yellow birch was collected on the upper slopes of Mt. Pisgah in western North Carolina, though he stated that it ranges to Quebec and northern Michigan. Britton (1908) further distinguished the two yellow birches on the basis of fruiting scale length. *Betula alleghaniensis* had short bracts, only 4 to 6 mm long, compared to bracts 8 to 10 mm long for *B. lutea.*

Blanchard (1911) drew attention to another yellow birch variant, a dark, tight-barked form, which he asserted had been confused with sweet birch in the north, northeast, and northwest. Fassett (1932) described the dark, tight-barked form as *Betula lutea* forma *fallax* and commented that such individuals perhaps form the basis of reports of sweet birch from Wisconsin. In their studies in Michigan, Dancik (1969) and Dancik and Barnes (1971) found that degree of exfoliation and bark color were not correlated with size and age. They attributed the variation to genetic differences among trees and concluded that the form was not worthy of any higher taxonomic status.

Whittaker (1956) found that both yellow birch and sweet birch

were apparently bimodally distributed along the elevational gradient in the Great Smoky Mountains. Both species also showed evidence of altitudinal differentiation. Whittaker suggested that the low-elevation yellow birch was *Betula alleghaniensis,* and the high-elevation yellow birch was *B. lutea,* the one found at more northerly latitudes.

Subsequent studies of range-wide or regional variation in natural stands of yellow birch have demonstrated significant differences over the range of the species in catkin, fruit, and bract characteristics, but no obvious geographic trends. Dancik and Barnes (1975) found significant differences in the variability of leaf characters among populations in the upper Great Lakes region. They also found that populations with a similar complex of site conditions shared similar leaf morphology. In a subsequent study of regional morphological variation, Sharik and Barnes (1979) sampled twenty-nine populations of yellow birch over five elevational transects from North Carolina to Vermont. They found significant differences among populations in leaf, catkin, bract, fruit, pollen, and bark attributes. Approximately 30% of the characters included in that study showed consistent trends with latitude or elevation.

Sharik and Barnes (1979) also reported regional variation in sweet birch in the Appalachians. Results were similar to those for yellow birch. There were significant differences between populations. More characters were significantly correlated with latitude in this species than in *Betula alleghaniensis,* although fewer (less than 20%) were correlated with elevation.

Although there is evidence of population differentiation in both species, few consistent geographic or environmental trends have been demonstrated. The broad geographic scope of the work discussed above and the extent of variation found over the ranges of the taxa may have concealed any trends that developed in response to environmental gradients. Because at least two investigators have asserted that two yellow birch taxa are present (and Whittaker equally strongly that there are two sweet birch ecotypes) in the southern Appalachians, it was concluded that a study based on intensive sampling in this relatively restricted area was needed to assess the nature and patterning of variation in both species. Specifically, the purpose of this study was to determine if the two species vary in a consistent fashion in their leaf, fruit, bract, or catkin morphology with elevation in the southern

Appalachians. The quantification of any discernible relationships with elevation and the comparison of patterns of variation in the two species over the elevation gradient was also of interest. Finally, if systematic patterns of variation do exist, are they sufficient to justify specific, subspecific, or varietal distinctions in either or both *Betula alleghaniensis* and *B. lenta*?

## METHODS

During the summer of 1979, populations of sweet birch and yellow birch were sampled at 52 different sites in North Carolina and adjacent parts of Tennessee, Georgia, and South Carolina (Table 1). Female catkins were collected from 134 of the 208 sweet birches sampled and 113 of the 310 yellow birches sampled. Sweet birch was sampled from 460 m to 1500 m, and yellow birch from 460 m to 1900 m. Yellow birch was sampled at 36 of the 52 sites, and sweet birch at 34 of the 52 sites.

Catkins were collected with pole pruners and measured before the samples were pressed and dried. All other measurements were made from pressed specimens. A list of characters measured and ratios derived from them is available from the senior author upon request. Most length measurements are as defined in Sharik and Barnes (1971). In addition to the 27 characters measured, 17 new variables were generated as ratios of the original characters.

Individual tree averages consisted of measurements from five leaves, usually one from each of five spur shoots, and five bracts and samaras taken from the central portion of one catkin. For catkin length and width, five catkins were usually measured, although for a few trees from one to four catkins were used. Gland concentration was the average number seen whole in ten fields of view at 100× magnification. Average stomate concentration was determined from ten fields of view at 450× magnification. Guard cell length was an average of five measurements taken between the third and fourth secondary vein of one leaf.

All statistical analyses were performed by computer programs in the SAS package (SAS Institute Inc., 1985a, 1985b). Summary statistics for each population, species means averaged across populations, and correlation coefficients of yellow and sweet birch morphological characters with elevation are available from the senior author upon request.

Voucher specimens are deposited at NCU.

Table 1. Population descriptions and number of trees sampled at each site for *Betula alleghaniensis* (yellow birch) and *B. lenta* (sweet birch). Numbers in parentheses are the number of fertile trees sampled out of the total number sampled to the left. The Blue Ridge Parkway is abbreviated BRP.

| | | | | | Sample Size | |
|---|---|---|---|---|---|---|
| No. | Pop. | County, State | Site Description | Elev. (m) | Yellow Birch | Sweet Birch |
| 1 | 6 | Rabun, GA | 0.7 mi. from GA/NC border on GA 28 | 700 | — | 5 (5) |
| 2 | 7 | Rabun, GA | 4.0 mi. from GA/SC border on GA 28 | 670 | — | 5 (4) |
| 3 | 14 | Rabun, GA | Tallulah R. just off US 23/441 | 520 | — | 5 (0) |
| 4 | 28 | Rabun, GA | Betty Cr. Rd. off US 23/441 | 700 | — | 5 (5) |
| 5 | 48 | Towns, GA | Brasstown Bald | 1430 | 16 (4) | — |
| 6 | 49 | Towns, GA | Brasstown Bald | 1130 | — | 5 (5) |
| 7 | 38 | Buncombe, NC | Milepost 394 on BRP | 670 | — | 5 (5) |
| 8 | 57 | Buncombe, NC | W slope of Craggy Dome | 1740 | 5 (3) | — |
| 9 | 35 | Caldwell, NC | Watauga/Caldwell Co. line on US 221 | 1220 | 29 (5) | 5 (5) |
| 10 | 9 | Clay, NC | Standing Indian Mtn. | 1650 | 10 (0) | — |
| 11 | 10 | Clay, NC | Standing Indian Mtn. | 1550 | 9 (0) | — |
| 12 | 11 | Clay, NC | Standing Indian Mtn. | 1490 | 10 (0) | 5 (0) |
| 13 | 13 | Clay, NC | Standing Indian Mtn. | 1400 | 10 (0) | — |
| 14 | 45 | Clay, NC | Forest Service Rd. 71 just off US 64 | 1100 | 21 (17) | 11 (11) |
| 15 | 16 | Haywood, NC | Richland Balsam Mtn. | 1890 | 4 (0) | — |
| 16 | 17 | Haywood, NC | Bear Pen Gap on BRP | 1710 | 5 (0) | — |
| 17 | 23 | Haywood, NC | Balsam Gap Overlook on BRP | 1100 | 29 (0) | 5 (0) |
| 18 | 25 | Haywood, NC | Waterrock Knob | 1800 | 5 (1) | — |
| 19 | 26 | Haywood, NC | Waterrock Knob | 1890 | 5 (0) | — |
| 20 | 53 | Haywood, NC | View of John Rock on BRP | 1620 | 5 (4) | — |
| 21 | 37 | Henderson, NC | Henderson/Transylvania Co. line on NC 280 | 670 | — | 5 (4) |
| 22 | 20 | Jackson, NC | 0.7 mi. from Macon/Jackson Co. line on US 64 | 1160 | 6 (1) | 5 (3) |
| 23 | 21 | Jackson, NC | Cashiers School on NC 107 | 1160 | 7 (5) | 5 (5) |
| 24 | 22 | Jackson, NC | 8.3 mi. N of Cashiers on NC 107 | 850 | — | 7 (5) |

Table 1. Continued.

| No. Pop. | | County, State | Site Description | Elev. (m) | Sample Size: Yellow Birch | Sample Size: Sweet Birch |
|---|---|---|---|---|---|---|
| 25 | 24 | Jackson, NC | Woodfin Cascades Overlook on BRP | 1400 | 5 (4) | 5 (5) |
| 26 | 59 | McDowell, NC | Milepost 348 on BRP | 1370 | 5 (3) | 5 (5) |
| 27 | 18 | Macon, NC | Along trail to Sunset Rock, Highlands | 1250 | — | 10 (0) |
| 28 | 27 | Macon, NC | Scaly Mtn. on NC 106 | 1040 | 5 (3) | 5 (5) |
| 29 | 39 | Macon, NC | Lake Sequoyah dam, Highlands | 1100 | — | 5 (0) |
| 30 | 40 | Macon, NC | Bridal Veil Falls, Cullasaja Gorge | 1040 | 5 (3) | — |
| 31 | 41 | Macon, NC | Entrance to van Hook Campground, Cullasaja Gorge | 980 | — | 10 (5) |
| 32 | 42 | Macon, NC | Cullasaja Gorge | 910 | 7 (4) | 5 (5) |
| 33 | 44 | Macon, NC | US 64 at Gold Mine Rd. | 850 | 7 (4) | 9 (6) |
| 34 | 46 | Macon, NC | 11.8 mi. N of Franklin on NC 28 | 640 | — | 5 (5) |
| 35 | 51 | Macon, NC | Highlands Biological Station | 1160 | 7 (7) | 8 (5) |
| 36 | 29 | Swain, NC | Along trail to Gregory Bald, Great Smoky Mtns. National Park | 730 | 13 (0) | 8 (0) |
| 37 | 31 | Swain, NC | Along trail to Gregory Bald, Great Smoky Mtns. National Park | 1130 | — | 5 (0) |
| 38 | 32 | Swain, NC | Along trail to Gregory Bald, Great Smoky Mtns. National Park | 1280 | 7 (0) | — |
| 39 | 33 | Swain, NC | Along trail to Gregory Bald, Great Smoky Mtns. National Park | 1490 | 8 (0) | — |
| 40 | 47 | Swain, NC | Nantahala R. | 520 | 13 (10) | 10 (10) |
| 41 | 64 | Swain, NC | Newfound Gap, Great Smoky Mtns. National Park | 1460 | 3 (1) | — |
| 42 | 36 | Transylvania, NC | 1.3 mi. E of Toxaway Falls on US 64 | 850 | — | 5 (5) |
| 43 | 52 | Transylvania, NC | 2 mi. N of Rosman on NC 215 | 730 | 5 (1) | — |
| 44 | 55 | Transylvania, NC | 1.2 mi. E of population 66 on US 276 | 670 | 7 (1) | 8 (0) |

Table 1. Continued.

| No. | Pop. | County, State | Site Description | Elev. (m) | Sample Size: Yellow Birch | Sample Size: Sweet Birch |
|---|---|---|---|---|---|---|
| 45 | 66 | Transylvania, NC | Coon Tree Picnic Area off US 276 | 670 | 4 (4) | — |
| 46 | 34 | Watauga, NC | 0.6 mi. NE of Julian Price Mem. Park, BRP | 1160 | 10 (5) | 5 (5) |
| 47 | 58 | Yancey, NC | Milepost 354 on BRP | 1580 | 5 (5) | — |
| 48 | 8 | Oconee, SC | 1.2 mi. from GA/SC border on SC 28 | 490 | — | 5 (0) |
| 49 | 60 | Sevier, TN | Along US 441 in Great Smoky Mtns. National Park | 460 | 5 (5) | 5 (5) |
| 50 | 61 | Sevier, TN | 5.8 mi. E of population 60 on US 441 | 980 | — | 5 (5) |
| 51 | 62 | Sevier, TN | 1.2 mi. E of population 61 on US 441 | 1100 | 6 (6) | 6 (6) |
| 52 | 63 | Sevier, TN | 2.1 mi. E of population 62 on US 441 | 1280 | 7 (7) | — |

## RESULTS

The two birch species differed significantly ($P < .01$ of equal species averages) in all but two of the characters used in this study. Blade width differed between the two taxa at a level of significance of .02. The two birches did not differ in their tendency toward cordiform samaras.

There were significant differences in the amount of variation in some characters between the two species. This was determined by calculating a folded F statistic under the assumption of equal variances (SAS Institute Inc., 1985b). Twenty-six characters (21 of them reproductive characters) had significantly different species variances, with yellow birch always having the greater variance. Additionally, only three sweet birches were ciliate-bracted and none were pubescent-bracted, whereas yellow birch bracts averaged 30.2 cilia on a side and were on average moderately pubescent.

Most characters differed significantly among conspecific populations as determined by one-way analysis of variance. For yel-

low birch, in only five characters was none of the variation attributable to population differences. In sweet birch, no population effect was evident for eight characters. Nine of the 44 characters manifested a contrasting variation pattern in the two taxa; that is, some of the variation was partitioned among populations in one but not the other taxon.

Fifty-five percent of the characters were significantly correlated with elevation in sweet birch and 64% in yellow birch ($P < .05$). All leaf size characters and most bract size characters were negatively correlated with elevation in both species. In yellow birch the fruits tended to be smaller at higher elevations. In sweet birch the samara body or seed tended to decrease in size as well, but samara size was not correlated with altitude. One might have expected, then, wider wings at higher altitudes or possibly a more cordiform samara. However, there was no evidence of a trend in either character.

In general, the two birches exhibited similar trends; there were some differences. Sweet birch serrations become finer at higher elevations and their bracts become more cruciform. The shorter sweet birch bracts at higher altitudes are due to shorter central lobes, whereas in yellow birch, shorter bract bases and central lobes contribute almost equally to reduce bract length. The samara wings of yellow birch are narrower at higher altitudes and the samara body more ovate.

In order to relate elevation to birch morphology, the eleven measured leaf characters for each population were subjected to a principal component analysis utilizing a correlation matrix for each species. No ratios were used in any principal component analysis. The principal component procedure has the effect of summarizing and reducing the variation of many variables into fewer synthetic variables called principal components. By condensing the variation into fewer variables, detection of factors correlated with the major aspects of sample variation is facilitated. In practice, only the first three principal components are considered biologically relevant. For sweet birch, 49% of the variation in the eleven leaf characters was explained by the first principal component (PRIN1). For yellow birch, 54% of the variation was explained by PRIN1. Figure 1 shows the PRIN1 values for each population plotted against elevation. Both plots depict linear relationships significant at $P \leq .0005$.

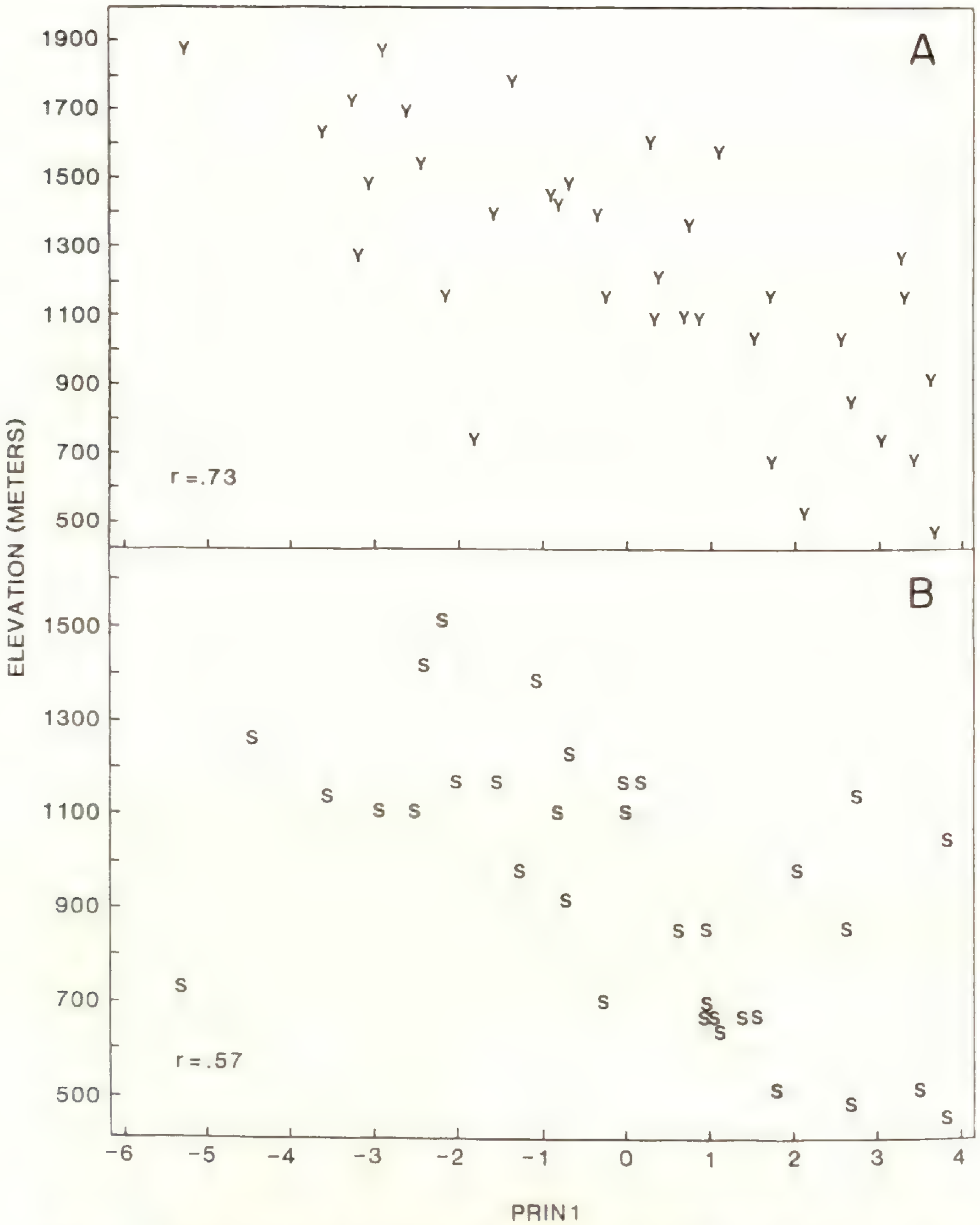


Figure 1. Relationships between population position on the first principal component (PRIN1) and elevation. **A.** For 36 populations of *Betula alleghaniensis*. **B.** For 34 populations of *B. lenta*.

When fruit and bract measurements were also used in the principal component analysis, and the PRIN1 values subsequently plotted against elevation, stronger linear relationships were discerned for each taxon. The sweet birch correlation coefficient (*r*) increased from .57 to .69; the yellow birch *r* value increased from

.73 to .82. Since 13 sweet birch populations and 15 yellow birch populations lacked a complete set of fruit and bract measurements, these results are not graphically illustrated here.

Although the relationship of elevation with birch morphology is predominantly linear, a few quadratic effects were associated with yellow birch fruit and bract characters. The quadratic effects on samara width, bract cruciformity, relative bract central lobe length, and wing width were due to these characters reaching their maximum values in populations between 900 m and 1200 m rather than in populations below 900 m. Populations below 1200 m tended to be more similar to each other in bract base length and samara size than did populations above 1200 m.

## DISCUSSION

The results indicate that Britton in 1904 collected yellow birch from one extreme of a clinal pattern of morphological variation. Indeed, he stated that he sampled trees from the upper slopes of Mt. Pisgah, which would put the site above 1500 m. His taxon, *Betula alleghaniensis,* was smaller in stature than *B. lutea,* with bracts shorter than 6 mm and leaves with cordate bases. Our lowest sample average for bract length was 4.3 mm from population 57. Populations 25, 63, and 64 also contained individuals with bract lengths of less than 6.0 mm. In general, high-elevation yellow birches tend to be smaller in habit than their low-elevation counterparts, a condition which is typical of orchard-type vegetation (Braun, 1950). Though Britton characterized his taxon as having a cordate leaf base, the plate of *B. alleghaniensis* in his *North American Trees* (1908) clearly shows cuneate leaf bases. This character is consistent with the data presented here, in that our leaf base character did not vary in a systematic fashion.

Britton (1904) further diagnosed his yellow birch as having bark either yellowish-gray or close and furrowed. We have observed a wide range of variation in the bark of southern Appalachian yellow birch. Many individuals have tight bark tending towards gray or brown. Population 45 is particularly well endowed with this bark variant. Fassett (1932) described a dark, tight-barked variant from Wisconsin as forma *fallax*; the range of this form is, then, extended from Wisconsin, Michigan, Indiana, and Ohio (Clausen, 1973) south to include North Carolina. On the other hand, lighter

Table 2. Species means for ten *Betula alleghaniensis* morphological characters as calculated by four different sources. All values are in millimeters.

| Character | Range Wide[a] | Western Great Lakes[b] | Appalachians[c] | Present Study: Populations Below 1200 m | Above 1200 m |
|---|---|---|---|---|---|
| Blade length | — | 109.5 | 106.0 | 109.6 | 92.6 |
| Blade width | — | 63.2 | 58.2 | 58.9 | 50.8 |
| Petiole length | — | 16.6 | 13.9 | 13.7 | 10.6 |
| Blade length II | — | 46.7 | 43.9 | 49.4 | 41.2 |
| Vein pairs | — | 14.5 | 15.2 | 15.0 | 14.4 |
| Bract length | 8.0 | — | 9.3 | 9.5 | 7.0 |
| Bract base length | 5.5 | — | 6.1 | 5.6 | 3.9 |
| Bract width | 5.9 | — | 6.8 | 7.5 | 6.2 |
| Seed length | 3.2 | — | 3.5 | 3.2 | 2.9 |
| Seed width | 1.8 | — | 1.7 | 1.7 | 1.7 |

[a] Clausen, 1968.
[b] Dancik and Barnes, 1975.
[c] Sharik and Barnes, 1979.

than typical silvery-barked yellow birches, common in New England (Clausen, 1973), were well represented in population 16.

In neither species did we find evidence of the bimodal pattern of distribution with elevation reported by Whittaker (1956). Moreover, his observation that high- rather than low-elevation yellow birch is more similar to the yellow birch of more northerly latitudes is contradicted by our data. Table 2 lists the species means for ten morphological attributes as calculated from four different collections. All but samara body width are negatively correlated with elevation in the southern Appalachians. This finding means that the averages for higher-elevation populations are less than the species average for these nine characters. It is the low-elevation southern Appalachian *B. alleghaniensis* that is more similar to the northern form, at least in its leaf, bract, and fruit morphology.

A number of discrepancies exist between our findings and those of Sharik and Barnes (1979). They found sweet birch samara width and samara body width increased with increasing elevation. We found both characters to vary independently of elevation. Samara length and samara body length varied independently in Sharik and Barnes' study but are negatively correlated here. Whereas we found secondary vein number in yellow birch to decrease at higher

altitudes, Sharik and Barnes found it to increase. Sweet birch petiole length was not related to elevation in the earlier study and is negatively correlated in ours. We did not find a significant trend in sweet birch leaf base shape as Sharik and Barnes did. From their complex data set, Sharik and Barnes concluded that trends in morphological variation occurring with changes in elevation do not necessarily occur in a similar manner throughout the Appalachians. Our results support this conclusion.

Some trends were consistent. The two birches are relatively smaller leaved at higher elevations throughout the Appalachians. Sweet birch has relatively smaller teeth at higher altitudes over its entire range. Yellow birch samara wings become narrower with increasing elevation.

In assessing regional morphological variation, we found southern Appalachian levels of variability to approximate or exceed levels elsewhere. For example, the range of population means for yellow birch blade length is 13 mm greater in the southern Appalachians than in the western Great Lakes region (Dancik and Barnes, 1975). Of the eight characters used here that were also used in the western Great Lakes study, five had greater ranges of population means in the present study, even though the present study is smaller both in number of trees and number of populations sampled. The fact that for eighteen characters used in both studies more variation was also found in our regional study than was found by Sharik and Barnes (1979) throughout the Appalachians suggests that elevational amplitude helps maintain variability.

Levels of variability also differ between the species. Our results show that yellow birch is significantly more variable than sweet birch in 28 of the 44 characters analyzed. In no character was sweet birch significantly more variable. Since the comparison is between a hexaploid, yellow birch, and a diploid, sweet birch (Woodworth, 1929), our findings support the long held supposition that polyploids possess greater ecological and genetic amplitude and, therefore, exhibit greater variability than related diploids (Stebbins, 1966; Porter, 1967; Jackson, 1976). There appears to be consistency within the genus in this regard. The tetraploid *Betula pubescens* Ehrh. is reported to be more variable than its nearest diploid relative, *B. pendula* Roth (Gardiner, 1984).

Our results do not support the integrity of Fernald's (1922) long bracted variety of yellow birch, *Betula alleghaniensis* var. *mac-*

*rolepis* (Fern.) Brayshaw. Variety *macrolepis* was distinguished by its 8 to 13 mm long fruiting bracts. Thirteen of the yellow birch populations we studied include some individuals with average bract lengths less than 8 mm and some with average bract lengths in excess of 8 mm. Because of the gradual nature of the morphological cline in both species and the variability maintained at any given elevation (Figure 1), we agree with Clausen (1973) and Hardin (1971) and find no validity to varietal distinctions in yellow birch.

Clinal patterns of variation have been reported in a number of eastern North American woody species. Kellison (1968) and Mercer (Master's thesis, N.C.S.U., Raleigh, 1969) demonstrated morphological character clines in *Liriodendron tulipifera* L. and *Fagus grandifolia* Ehrh., respectively, from the mountains to the coast of North Carolina. McDougal and Parks (1984) sampled *Quercus rubra* L. over an elevational transect in the southern Appalachians and documented a flavonoid chemical cline in that species. Fryer and Ledig (1972) reported morphological and physiological clines in *Abies balsamea* (L.) Mill. over an elevational transect in the White Mountains of New Hampshire. Relationships with elevation in the White Mountains have also been reported for *Acer saccharum* Marsh. leaf morphology and rates of photosynthesis and respiration (Ledig, 1971; Ledig and Korbobo, 1983).

In Scotland, *Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman becomes smaller leaved with increasing altitude. Gardiner (1984) applied the varietal name, *microphylla,* to this small leaved, high-elevation birch and stated that it is apparently "genetically stable." On the high mountain peaks of the northern Appalachians, *Betula cordifolia* Regel is a component of the krummolz (elfinwood) vegetation. The clinal pattern of variation described here appears to be common in the genus. It cannot, however, be stated that it is a general phenomenon in the southern Appalachians. Braun (1950) noted that dwarfing is sometimes conspicuous on the windswept ridge crests of southern Virginia and Tennessee. She observed not only greatly reduced stature, but also reduced leaf size in sweet birch and other species. Mercer (Master's thesis, N.C.S.U., Raleigh, 1969), however, reported that *Fagus grandifolia* was larger leaved at higher elevations in North Carolina. Patterns of variation depend on the racial history of a taxon as well as environmental influence.

Though environment certainly influences phenotypic expres-

sion of birch genotypes, it is not unlikely that the observed patterns of variation have genetic components. In another study (unpubl.) sweet and yellow birches grown from seed collected at different elevations in the southern Appalachians were planted outside in Chapel Hill in 1979 and 1980. In April, 1984, bud expansion data were taken on these birches. Our preliminary analyses agree with Clausen (1973) and show that high-elevation birches leaf out later than low-elevation birches and that this trait is genetically controlled. Our observations of flowering phenology in the Chapel Hill plots agree closely with our bud expansion data.

Gene flow via pollen migration, then, may be partially restricted on the southern Appalachian mountain slopes. Genes controlling morphological traits in high-elevation populations at least could differ in their allelic composition from those in low-elevation populations. It is not possible, from our phenological data or from our observations of natural stands, to measure the length of the flowering period in the mountains or the extent of flowering overlap or even synchrony at different elevations on one mountain slope. Such things certainly vary from year to year and slope to slope. However, from our observations of flowering phenology in natural stands, it appears that birches growing below 600 m seldom if ever cross with birches growing above 1500 m. This moderate level of genetic isolation may have allowed sufficient genetic differentiation to bring about the observed pattern of morphological variation.

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# THE ORCHID GENERA *ONCIDIUM* SW. AND *TOLUMNIA* RAF. IN FLORIDA

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## ABSTRACT

The current taxonomic, ecological, and distributional statuses of the genera *Oncidium* Sw. and *Tolumnia* Raf. in Florida are discussed. Descriptions and a key to the three species, *O. floridanum, O. undulatum,* and *T. bahamense,* are included. *Oncidium undulatum* is neotypified and *O. carthagenense* is excluded from the flora of Florida.


Key Words: *Oncidium, Tolumnia, O. altissimum, O. bahamense, T. bahamense, O. carthagenense, O. ensatum, O. floridanum, O. luridum, O. undulatum, O. variegatum,* Orchidaceae, Florida

## INTRODUCTION

Four species of *Oncidium* Sw. have been reported from Florida (Ames, 1924; Small, 1933; Correll, 1950; Luer, 1972; Long and Lakela, 1976): *Oncidium bahamense* Nash ex Britt. & Millsp.; *Oncidium carthagenense* (Jacq.) Sw.; *Oncidium floridanum* Ames; and *Oncidium luridum* Lindl. Small (1913b, 1933) reported the last of these species as *O. undulatum* (Sw.) Salisb., while Beckner (1964) incorrectly reported it as *O. cosymbeforum* Morren, a synonym of *O. luridum. Oncidium luridum* is a central American species, but the name has been misapplied to Florida and Caribbean populations of what is correctly *Oncidium undulatum* (Sw.) Salisb., as reported by Small (1913b, 1933). *Oncidium bahamense* has been removed from the genus *Oncidium* and placed in the genus *Tolumnia* Raf. (Braem, 1986). *Oncidium carthagenense,* erroneously included by Small as part of the flora of Florida, is excluded.

As a result of these changes, the genus *Oncidium* in Florida is now represented by two species, *O. floridanum* and *O. undulatum,* and the genus *Tolumnia* is represented by one species, *T. bahamense* (Nash ex Britt. & Millsp.) Braem.

## KEY TO THE SPECIES OF *ONCIDIUM* AND *TOLUMNIA* IN FLORIDA

1. Pseudobulbs inconspicuous, poorly developed; leaves triquetrous, margin serrulate; lateral sepals connate nearly to apex ..... **3.** *Tolumnia bahamense*

1. Pseudobulbs large, compressed; leaves conduplicate to flat, margin entire; lateral sepals free ..... 2
   2. Leaves coriaceous, narrowly linear-oblong to ligulate, arising from apex and surrounding sheaths, apically to three-leaved ..... **1.** *Oncidium floridanum*
   2. Leaves coriaceous and rigid, broadly oblong-elliptic to linear-elliptic, solitary leaf at apex ..... **2.** *Oncidium undulatum*

## DESCRIPTIONS AND DISCUSSION

1. **Oncidium floridanum** Ames, Sched. Orch. 7: 13. 1924. Figure 1. TYPE: Florida, Dade Co., *Eaton 957* (HOLOTYPE: AMES).

Plants terrestrial, epilithic or epiphytic, to 1.45 m tall. Roots numerous, thick, canescent to velamentous. Rhizome short, stout, creeping or ascending, enclosed by scarious imbricating sheaths. Pseudobulbs clustered, oblong to ovate, compressed, ancipitous, to 1.4 dm long, 5 cm wide, partially enveloped by 3–6 distichous leaf-bearing sheaths, with 1–3 apical leaves. Leaves coriaceous, narrowly linear-oblong to ligulate, subobtuse to acute, to 1.05 m long, 2.5 cm wide. Peduncle slender, suberect, distantly several sheathed. Inflorescence lateral, to 1.42 m tall, racemose to paniculate above, to 85-flowered. Floral bracts ovate to lanceolate, acute to acuminate, to 8 mm long, 2 mm wide. Ovary pedicellate, slender, to 2.6 cm long. Sepals yellow with brown spots, lanceolate to elliptic, acute, basally clawed to attenuate, concave, the margins undulate, to 1.8 cm long, 4 mm wide. Petals yellow with brown spots, ovate to elliptic, acute, basally clawed, the margins undulate, to 1.4 cm long, 5 mm wide. Labellum three-lobed, yellow, to 1.4 cm long, 9 mm wide, the lateral lobes basal, orbicular, obtuse, the margins reflexed, entire or crenulate, the midlobe separated from the lateral lobes by a short isthmus with brown spots, midlobe cordate to reniform, shallowly emarginate with apicule in sinus, the margin entire or crenulate, the callosity on isthmus variable, yellow-orange with reddish-brown spots, provided with 2–4 anterior and 2–4 posterior tubercles connected by a central ridge. Column short, erect, to 5 mm long, 2 mm wide, with expanded lateral wings projecting from the apex, yellow, ligulate, the margins crenulate, to 2 mm long, 1 mm wide, anther yellow. Capsule pendent, elliptic, to 3 cm long, 2 cm thick.

Figure 1. *Oncidium floridanum* Ames. **A.** Flowering plant. **B.** Flower, frontal view. **C.** Sepals, petals, and labellum, frontal view.

*Oncidium floridanum* was first found in Florida by Small and Carter in 1903, between Cutler and Black Point, Dade County, Florida (Correll, 1950). It was very common in the tropical hardwood hammocks of southern Dade County and in the cypress swamps, sloughs, and hammocks of Monroe and Collier Counties.

However, the replacement of the hammocks in southern Dade County by housing developments, and collection of the orchids in hammocks outside the boundaries of the Everglades National Park, has virtually eliminated the species from these areas. *Oncidium floridanum* was also common in the Big Cypress swamp in Collier and Monroe Counties. However, drastic changes in the water flow in the Big Cypress swamp caused by diverting the natural sheet flow of water into canals to supply a burgeoning human population in southern Florida have dramatically lowered water levels and allowed fires to penetrate deep into the cypress heads and hardwood hammocks that are characteristic of this area. This orchid often grew just above the high water mark on trunks of larger cypress trees. Areas which had large numbers of this orchid, especially in the vicinity of Monument Road in Collier County, now are virtually devoid of it. Fortunately *O. floridanum* is still relatively common in the hammocks and sloughs of Everglades National Park; it is one of the most common orchids in the Bahama Archipelago and has been also reported from Cuba by Liogier (1969).

Luer (1972) and others have proposed that *Oncidium floridanum* may be conspecific with the Guatemalan species, *O. ensatum* Lindl. An examination of a photograph of the holotype of *O. ensatum* from Kew revealed that both species are vegetatively very similar but exhibit many distinct floral differences. These differences were even more evident when we examined living material from Guatemala obtained from Marvin E. Ragan of Orange Park, Florida. The sepals and petals of *O. floridanum* are yellow with brown spots, lanceolate or ovate to elliptic, narrowly acute and the margins are flat or undulate. In *O. ensatum* the sepals and petals are dark brown, broadly elliptic, subacute to abruptly acute and the margins are revolute. The isthmus of the labellum of *O. floridanum* is yellow with brown spots, in *O. ensatum* the isthmus is dark brown. The midlobe of the labellum of *O. floridanum* is cordate to reniform and concave, the midlobe of the labellum of *O. ensatum* is broadly elliptic, bilobed, and the margin is revolute. The callosity is variable in both species, however the tubercles are more numerous and thicker in *O. ensatum*.

2. **Oncidium undulatum** (Sw.) Salisb., Trans. Hort. Soc. London. 1: 295. 1812. Figure 2. BASIONYM: *Epidendrum undulatum* Sw., Prod. Veg. Ind. Occ. 122. 1788. TYPE: In the absence

of any material verifiable as the holotype, we here designate the Burmann plate cited by Swartz in his protologue as the neotype: Plantarum Americanarum Fasciculus, p. 173, t. 178, f. 2, 1758.

Plants epiphytic, rhizomatous, to 5 m tall. Roots numerous, thick, canescent to velamentous. Rhizome short, stout, ascending, enclosed by scarious imbricating sheaths. Pseudobulbs cylindric, to 5 cm long, 4 cm thick, concealed by 3–4 imbricating sheaths, with 1 apical leaf. Leaf coriaceous, rigid, broadly oblong-elliptic to linear-elliptic, obtuse to acute, to 1.05 m long, 2.8 dm wide. Peduncle slender, erect to suberect, distantly several-sheathed, the sheaths tubular, appressed, acute, to 2 cm long. Inflorescence lateral, to 2.65 m long, racemose to paniculate above, usually with short lateral branches bearing 2–4 flowers, to 85-flowered. Floral bracts triangular-lanceolate, acute to acuminate, to 1.3 cm long. Flowers dull yellow to greenish-yellow with dark reddish-brown spots. Sepals free, clawed, the dorsal sepal spatulate to obovate, the apex rounded to obtuse, margin undulate, occasionally involute, to 1.8 cm long, 6 mm wide. Lateral sepals spatulate, to obovate, obtuse, the margin undulate, to 2 cm long, 9 mm wide. Petals clawed, to 1.8 cm long, 7 mm wide, lamina orbicular to oblong, truncate to rounded, the margin undulate-crenulate. Labellum pandurate, 3-lobed, to 2 cm long, 1.5 cm wide, lateral lobes basal, obtuse, the margins revolute, midlobe separated from lateral lobes by a short isthmus, midlobe reniform, entire to crenulate, callosity on isthmus is five fleshy lobes which are tuberculate, yellow in center with purple and white staining. Column white, stained with purple, erect, to 6 mm long, 3 mm thick, with bilobate wings at apex. Capsule ellipsoid, to 4 cm long, 2.5 cm thick.

*Oncidium undulatum* was first discovered in Florida by Eaton and Soar in 1903 (Correll, 1950) and erroneously identified first by Small (1913a) as *O. guttatum* (L.) Reichenb. f. and *O. luridum* Lindl. by Ames (1924), Correll (1950), and Luer (1972). A comparison of a photograph of the holotype of *O. luridum* (K-L) and living material of *O. luridum* from Central America, with living material of *O. undulatum* from Florida and Jamaica, unequivocally demonstrated that *O. luridum* and *O. undulatum* are not conspecific.

Vegetatively both *Oncidium undulatum* and *O. luridum* are

Figure 2. *Oncidium undulatum* (Sw.) Salisb. **A.** Flowering plant. **B.** Flower, frontal view. **C.** Sepals, petals, and labellum, frontal view.

similar, although *O. undulatum* has consistently longer and wider leaves. Florally they are very distinct. The inflorescence of *O. undulatum* is usually twice as long (up to 2.5 m long) as *O. luridum*. The flowers are also larger in *O. undulatum*. The flowers of *O. undulatum* are uniformly yellow with distinct reddish-brown spots. The flowers of *O. luridum* are a yellowish-brown with brown blotches that usually overlap and the labellum is brownish-orange

without spots. The differences in the labellum, especially the shape of the crest, are the main characters separating the two species. Both species have reniform midlobes; however, *O. luridum* is more broadly reniform, appearing elliptic, while *O. undulatum* is narrowly reniform, appearing orbicular. The margin of the midlobe of the labellum of *O. undulatum* is undulate while the margin of the labellum of *O. luridum* is flat. The callosity on the isthmus of *O. undulatum* consists of five fleshy, centrally-located, tuberculate lobes which are yellow with purple and white staining, while the callosity on *O. luridum* consists of four large, fleshy, tuberculate lobes connected by a central fleshy keel, all of which are yellow with red and white staining. The wings on the apex of the column of *O. undulatum* are broad and bilobed; the wings of *O. luridum* are narrow and not bilobed. Additionally the sepals and petals of *O. undulatum* have a long, slender claw and are spatulate to obovate, while the sepals and petals of *O. luridum* have a short claw and are obovate to broadly elliptic.

The name *Oncidium altissimum* (Jacq.) Sw. was considered an earlier name for *O. luridum* and therefore applied to the Florida population (Garay and Stacy, 1974). A careful analysis of a photograph of the specimen at BM which Jacquin had in his possession when he described *O. altissimum* and Jacquin's illustration of *O. altissimum* (Select. Stirp. Amer. Hist. 229, t. 141, 1763) clearly demonstrates that it is not conspecific with *O. luridum* or *O. undulatum*. *Oncidium luridum* and *O. undulatum* are in the section *Miltoniastrum* Reichb. f., which is characterized by plants having a single apical leaf which is broad, thick, rigid, and coriaceous. *Oncidium altissimum* is the type of the genus and is therefore in the section *Oncidium*. This section contains the bulk of the plants in the genus and is characterized by plants which have 1–3 apical leaves and 2–5 leaf-bearing sheaths which partially conceal the pseudobulb. The leaves are narrow, elongated, and linear. Most of the confusion surrounding the application of the name *O. altissimum* to the Florida population stems from Jacquin (Enum. Syst. Pl.: 30, 1760) who incorrectly cited a Sloane plate (Hist. Jam.: t. 148, f. 1, 1707) as a synonym. This plate illustrates a plant from Jamaica which represents the same species as the Florida population. The Sloane plate, however, does not represent the same species as the specimen Jacquin used to describe *O. altissimum*.

Although several names can be found in the literature which

apply to the Florida population, the earliest available name is *Oncidium undulatum* (Sw.) Salisb. When Swartz (Prod. Veg. Ind. Occ. 122, 1788) described this species as *Epidendrum undulatum,* he cited several elements including a Burmann plate (Pl. Amer. Fasc. 173, t. 178, f. 2, 1758), and the same Sloane plate Jacquin incorrectly cited as a synonym of *O. altissimum.* Sloane's description of the foliage (Hist. Jam.: 250, 1707), which is absent from both the plate and the specimen in the Sloane herbarium from which the plate was illustrated, does not match the foliage of plants from Jamaica or Florida. Although we feel that the Sloane plate probably represents *O. undulatum,* the absence of any foliage on the plate makes it a poor element upon which to base a species. The Burmann plate, however, unequivocally matches both the floral and vegetative characteristics of plants from Florida and Jamaica. After a careful search of the major herbaria in Europe we were unable to locate a specimen which Swartz may have used when describing *E. undulatum.* We are therefore designating the Burmann plate as the neotype for *Oncidium undulatum* (Sw.) Salisb.

Several authors (Ames, 1924; Correll, 1950; Luer, 1972) cited Swartz's *Epidendrum undulatum* as a synonym for *Oncidium luridum*; Luer (1972) also cited it as a synonym of *O. carthagenense.* But Swartz published the epithet *undulatum* in 1788, prior to the publication of *O. luridum* in 1823. J. K. Small (1913b, 1933) was the only author to use *O. undulatum* for the Florida population, recognizing that *O. luridum* was a distinct species.

In Florida, *Oncidium undulatum* is presently restricted to the Everglades National Park where it is locally abundant, occurring along the edges of many of the brackish creeks, small lakes, and ponds that are an integral part of most of the habitats in the southern part of the park.

3. **Tolumnia bahamense** (Nash ex Britt. & Millsp.) Braem, Orchidee (Hamburg) 37(2): 59. 1986. Figure 3. TYPE: Grand Bahama Island, Bahama Islands, *Brace 3689* (HOLOTYPE: NY; ISOTYPES: F, US).

Plants epiphytic or terrestrial, rhizomatous, to 6.5 dm tall. Roots numerous, slender, canescent to velamentous. Rhizome stoloniferous, repent, decumbent, wiry, remotely several-sheathed, the sheaths scarious, ovate-triangular, acute, to 1.1 cm long, 4 mm

wide. Pseudobulbs remotely produced, to 1.2 dm apart, to 9 mm long, 4 mm wide, flattened, completely enclosed by 5–10 distichous leaves. Leaves coriaceous, distichous, imbricated, produced at intervals along pseudobulb, olive-green to bronzy-purple, conduplicate, recurved, lanceolate, acute, to 1.4 dm long, 8 mm wide, the margins cartilaginous and serrulate. Penduncle slender, erect, distantly several-sheathed. Inflorescence lateral, to 6.4 dm tall, racemose or rarely paniculate above, to 25-flowered. Floral bracts minute, lanceolate, acute, to 2 mm long, 1 mm wide. Ovary pedicellate, slender, to 1.8 cm long. Sepals white to greenish-white, basal ⅔ with reddish-brown spots; the dorsal sepal spatulate, basally clawed to attenuate, concave, emarginate, acute or apiculate, to 4 mm long, 2 mm wide. Lateral sepals oblanceolate, concave, acute, connate nearly to apex, to 5 mm long, 3 mm wide. Petals white to greenish-white, basal ½ with reddish-brown spots or bars, spatulate to ligulate, basally clawed to attenuate, concave, acute, the margins undulate, to 6 mm long, 3 mm wide. Labellum three-lobed, white, occasionally with pink tint, to 1.2 cm long, 1.5 cm wide, the lateral lobes basal, linear-elliptic to orbicular, obtuse to broadly rounded, reflexed, margin irregularly crenulate, the midlobe separated from the lateral lobes by a short isthmus with brown spots, the midlobe reniform, cordate or broadly obovate, deeply emarginate, usually with an apicule in the sinus, the margin irregularly crenulate, the callosity on isthmus variable, yellow-orange with reddish-brown spots, usually provided with two anterior and three larger posterior tubercles. Column stout, erect, to 3 mm long, 2 mm wide, with expanded lateral wings projecting from apex, white or pink, ovate, base obtuse, apex acute, irregularly lobed, to 1.1 mm long, 0.6 mm wide, anther white, apex purplish-brown. Capsule pendent, to 1.5 cm long, 8 mm wide.

The genus *Oncidium* is divided into several clearly defined sections. Although the flowers of all oncidiums are very similar, thereby making sectional distinction using floral characteristics very difficult, vegetatively the sections are distinct. In addition, the sections have different chromosome numbers. These differences, together with their strictly Caribbean distribution, were the basis for the elevation of the section containing *Oncidium bahamense* to generic level (Braem, 1986). The earliest name available for the new genus was *Tolumnia* Raf.

*Tolumnia bahamense* was first discovered in Florida in 1904

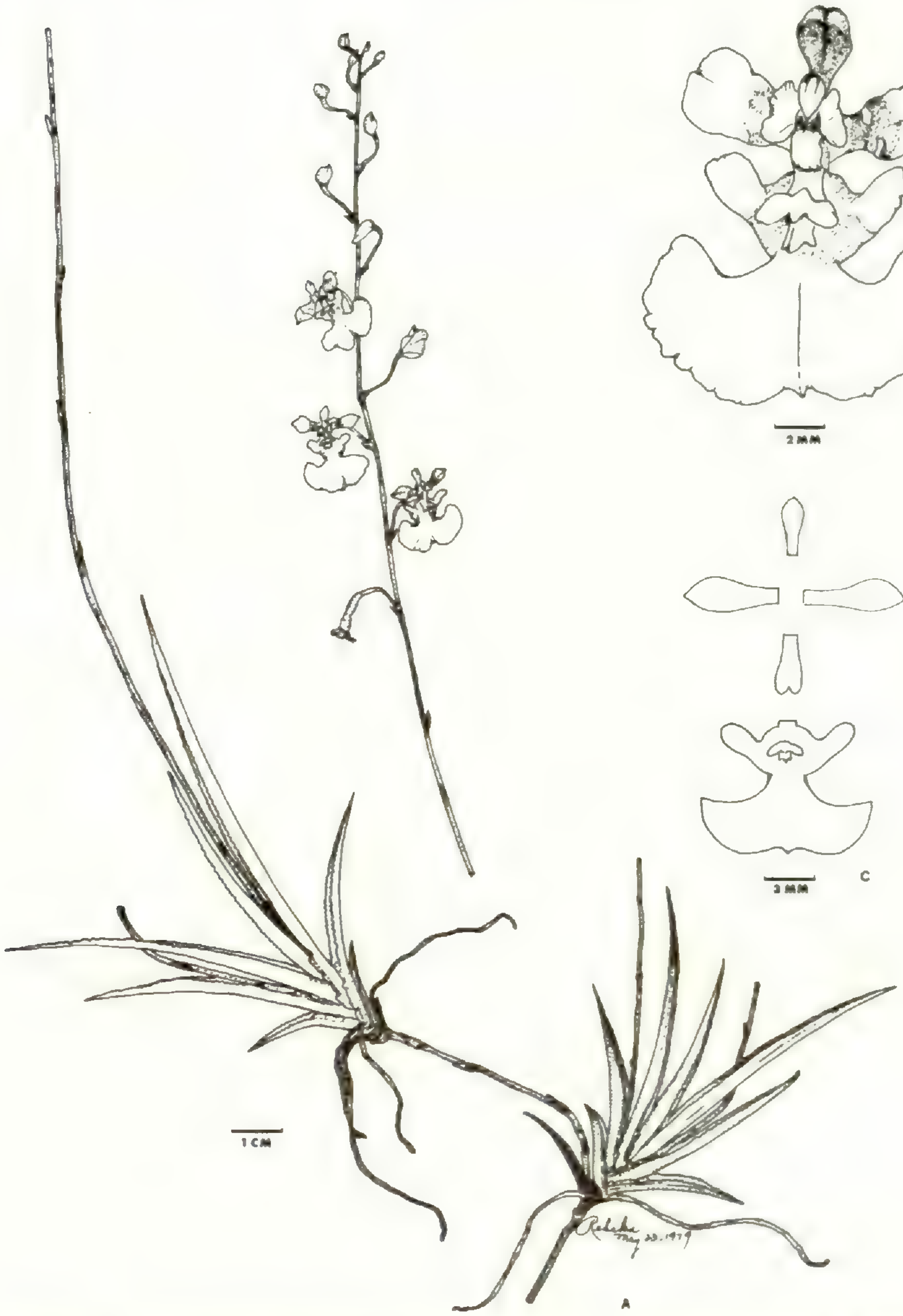


Figure 3. *Tolumnia bahamense* (Nash ex Britt. & Millsp.) Braem. **A.** Flowering plant. **B.** Flower, frontal view. **C.** Sepals, petals, and labellum, frontal view.

(Correll, 1950) and misidentified by several authors as *Oncidium variegatum* Sw. (Ames, 1905, 1924; Small, 1933; Correll, 1950). For many years the correct identification of this species was obscured by additional misidentifications by Moir (1962), until Luer (1972) finally established the correct epithet *bahamense.*

*Tolumnia bahamense* occurs in Martin and Palm Beach Coun-

ties. The largest population occurred in the xeric acid pine scrub surrounding the old Jupiter cemetery on County Line Road, which separates Palm Beach and Martin Counties. This area has been almost completely developed, leaving only a few isolated acres where several plants survive. However, these few remaining acres are in imminent danger of being cleared. A second large population once existed in the scrub, growing on the sand dunes just east of US 1 in southern Martin County. This population has been decimated by home-builders, by orchid collectors, and by periodic fires, and is now virtually extirpated. However, in the early 1960's a large number of plants were saved from destruction by transplantation from the cemetery area to three areas within the boundaries of Jonathan Dickinson State Park (Sauleda, 1986). Recently two populations have been discovered within the park. Apparently the transplanted plants have survived and established viable populations in an area where they will be safe from habitat destruction and orchid collectors.

The restricted distribution of *Tolumnia bahamense* in Florida, combined with the fact that it has a wide distribution in the Bahama archipelago, suggests that it may have been introduced into Florida (Sauleda and Adams, 1981). The Florida population occurs within approximately 120 km of the closest Bahamian population. While dispersal from the Bahama Islands to Florida may have been by natural means—storms, for example—it is more probable that Bahamian fishermen brought plants from the Islands and planted them on the graves of fellow fishermen buried in the Jupiter cemetery. The cemetery contains several headstones with names which are thought to be Bahamian.

*Tolumnia bahamense* flowers in April and May and can be detected in its natural habitat by its strong fragrance. It is one of the few tolumnias with fragrant flowers.

**Oncidium carthagenense** (Jacq.) Sw., Handl. Kongl. Svensk. Vetensk. Acad. 21: 240. 1800.

*Oncidium carthagenense* was reported in Florida (Correll, 1950; Luer, 1972) based upon a single specimen collected by J. K. Small in 1916. The collection locality, cited on the herbarium specimen at NY, is Coot Bay, Florida. After numerous trips to the Coot Bay area, during which careful searches were made, we were unable to locate any plants of this species. Therefore, we conclude

that this species does not occur in Florida. This conclusion is further supported by the fact that *O. carthagenense* had not been collected prior to the Small collection nor has it been collected since. The Small specimen does not have any foliage, and consists only of a partial inflorescence. It is likely that Small made this specimen from a plant in cultivation at the Deering Estate in southern Florida, where he kept many of the plants he collected until they flowered. Small also routinely grew plants sent to him from Central America at the Deering Estate. We are convinced that Small made the specimen, now at NY, from a plant he mistakenly believed was collected in Florida but which was actually collected in Central America. For these reasons we are excluding this species from the flora of Florida.

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# DISTRIBUTION OF GAMETOPHYTIC POPULATIONS OF *VITTARIA* AND *TRICHOMANES* IN PENNSYLVANIA

JAMES C. PARKS

## ABSTRACT

Fifty-eight of Pennsylvania's sixty-seven counties were surveyed for the presence of *Vittaria* and *Trichomanes* gametophytes. Sixteen new county records are noted for *Vittaria.* Five previous reports bring the total to twenty-one. *Trichomanes,* reported previously from twelve counties, is herein recorded from an additional thirty. Phytogeographical observations and comments for both taxa are included.

Key Words: *Vittaria, Trichomanes,* fern gametophytes, distribution

## INTRODUCTION

The Appalachian *Vittaria* gametophyte has presented to biologists intriguing taxonomic, ecological, and distributional problems ever since its discovery by A. J. Sharp and identification by Wagner and Sharp (1963). Gametophytes of four tropical fern genera, including *Vittaria* and *Trichomanes,* were reported by Farrar (1967) to be reproducing independently of their sporophytes in the southern Appalachians. Farrar (1974, 1978) described gametophytes of *Vittaria*; Farrar and Wagner (1968) described those of *Trichomanes. Vittaria* gametophytes are shaped like thalloid ribbons while those of *Trichomanes* form tufts of filaments. The prothallia of both are gemmiferous, permitting them to reproduce independently of their sporophytes. Farrar (1978, 1985) considered problems of species assignment, habitat characteristics, and biogeography of these Appalachian plants. Both *Vittaria* and *Trichomanes* gametophytes occupy a habitat characterized as humid, shaded grottoes in noncalcareous rock, usually sandstone. Sporophytes of neither *Vittaria* nor *Trichomanes* are known to occur naturally in Pennsylvania.

While Farrar et al. (1983) established the presence of *Vittaria* and *Trichomanes* gametophytes in the Pennsylvania flora, relatively few sites were reported. *Trichomanes* gametophytes are reported from as far north as central Vermont (McAlpin and Farrar, 1978; Farrar et al., 1983; Miller, 1984), but the northernmost station for *Vittaria* is in Chautauqua Co., New York (Parks and Farrar, 1984). This paper presents the results of the first

intensive distributional study for a large area within the range of these taxa. The Wisconsinan terminal moraines are extensive in Pennsylvania (Berg, 1980) (Figure 1); therefore, a distributional study of these taxa in this region should clarify the problem of postglacial re-establishment of these genera in glaciated areas, considered by Farrar et al. (1983). The northern range limits of the Appalachian *Vittaria* gametophyte are most likely to be clarified by field work in this state. This study was also undertaken to determine if these recent additions to the Pennsylvania flora should be considered rare or endangered taxa in the Commonwealth.

## METHODS

Fifty-eight of Pennsylvania's 67 counties were surveyed for the presence of *Vittaria* and *Trichomanes* gametophytes. By comparing an area on the Pennsylvania Geological Map (Berg, 1980) with the same one on a topographic map, locations containing rock exposures of a suitable substrate were located. Shaded grottoes in promising rock outcrops were explored extensively using a flashlight. When the plants were found, they were examined on site with a 10× lens, and a live specimen was collected. Specimens were later examined microscopically, dried, and deposited at MVSC. Appropriate geographic and ecological data were recorded and, at some sites where the plants were abundant, material was collected for laboratory culturing.

## RESULTS AND DISCUSSION

*Vittaria* gametophytes were collected from 18 sites representing 16 new Pennsylvania county records (Figure 1). Including five county records at six sites reported by Farrar et al. (1983), *Vittaria* gametophytes are now known from 21 counties and 24 sites in Pennsylvania. *Trichomanes* gametophytes were collected from 75 sites representing 30 new county records (Figure 1). In areas where *Trichomanes* sites are relatively abundant, contiguous but distinct stations are not plotted on Figure 1; however, they are included in a complete list of collection sites (including those cited in the text), available from the author. Farrar et al. (1983) reported *Trichomanes* from 12 counties at 17 sites. However, Dr. Frank Busor of East Stroudsburg University (pers. corr.) indicated that

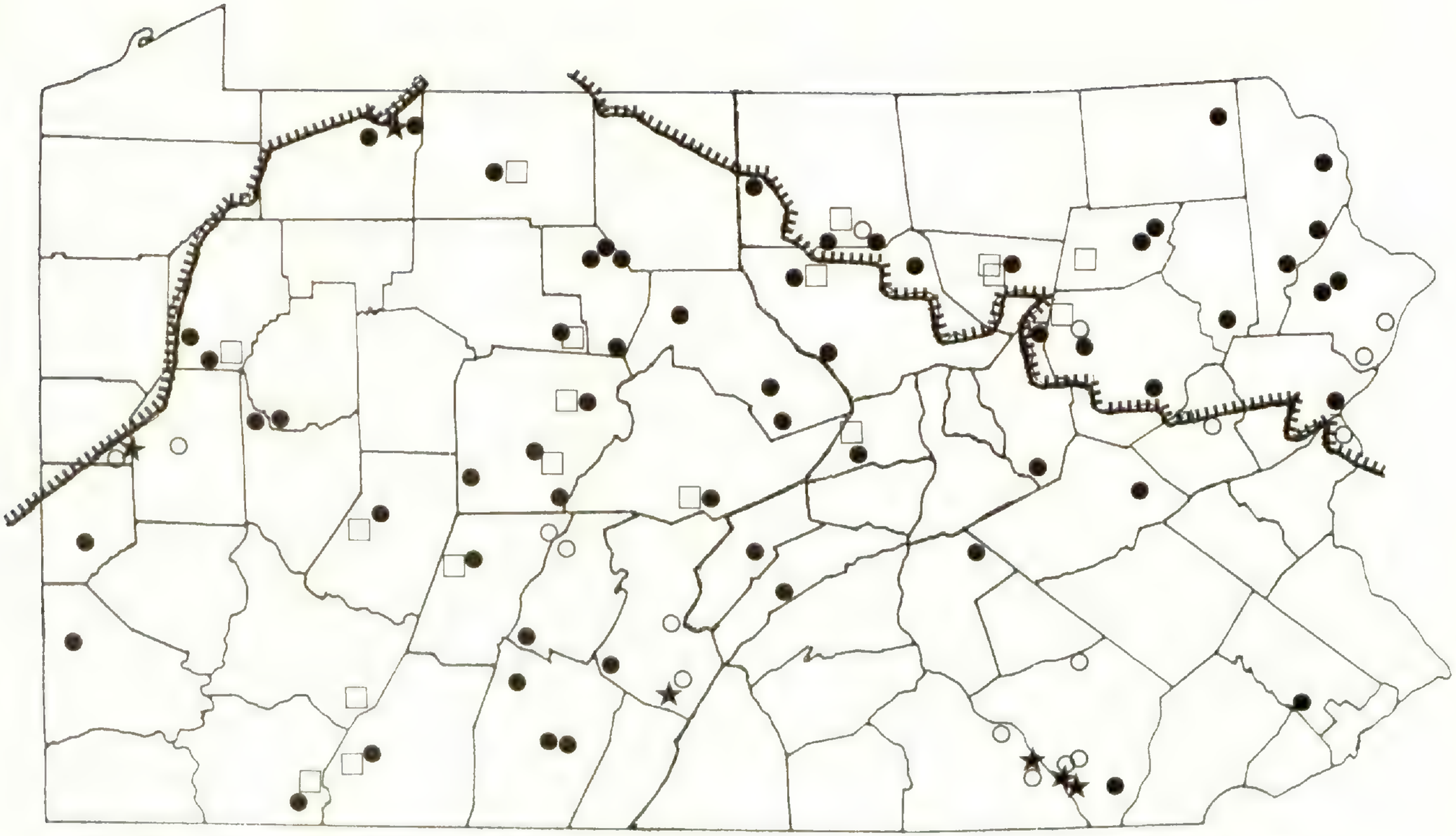

Figure 1. Distribution of *Vittaria* and *Trichomanes* gametophyte colonies in Pennsylvania. *Vittaria* stations from Farrar et al. (1983) ★; new records □. *Trichomanes* stations from Farrar et al. (1983) ○; new reports ●. Hatched line indicates the limits of Wisonsinan glaciation.

the site reported for Monroe Co. would have to be in Northampton Co., as the substrate mentioned, Martinsburg Shale, does not occur in Monroe Co. This information is confirmed by study of the Pennsylvania Geological Map (Berg, 1980). As I have collected *Trichomanes* in Monroe Co. (*Parks 4339*), amending Farrar's site to Northampton Co. adds that county to those wherein *Trichomanes* grows. In total, *Trichomanes* gametophytes are now noted from 76 sites in 42 Pennsylvania counties.

The ecological requirements of *Vittaria* and *Trichomanes* gametophytes are evidently similar, as I have found them growing in close proximity at many sites (e.g., *Parks 4299* and *Parks 4300* in McKean Co., *Parks 4334* and *Parks 4335* in Somerset Co., *Parks 4551* and *Parks 4552* in Clearfield Co.). However, differences observed and reported below may prove helpful in locating these plants and in understanding their distribution. When the two were observed at the same site, they were usually growing in different rock crevices or overhangs. *Vittaria* is generally found at the very back of rock crevices but is sometimes observed as mats on the lower rock surface. The prothallia may be growing as little as 15–30 cm from the face or as far back as a 13 m (*Parks 4404* in Indiana Co.). *Trichomanes* gametophytes are usually hanging down in tufts from the upper surface of the rock crevice or on a vertical wall in a narrow crack. While *Trichomanes* is often found at *Vittaria* sites, it has been found frequently by itself on smaller exposures, at sites subject to more desiccation, and on a greater variety of rock types including shales (*Parks 4403* in Indiana Co.).

The distribution of *Vittaria* gametophytes in Pennsylvania relative to the Wisconsinan glacial moraines is different than that of *Trichomanes*. I have found *Trichomanes* at numerous sites in the glaciated Pocono Mountains (Figure 1) but I have not recovered *Vittaria* from this region. I have discovered five *Vittaria* sites in glaciated parts of Pennsylvania (Figure 1), all of them 30 km or less north of the Wisconsinan terminal moraines (cf. Crowl and Sevon, 1980). Of the two previous reports, one station in Ohio is ca. 90 km into glaciated terrain (Cusick, 1983) and one in New York is ca. 19 km north of the Wisconsinan terminal moraine (Parks and Farrar, 1984). These results indicate that the northern range limits of the Appalachian *Vittaria* gametophyte parallel closely the Wisconsinan terminal moraines. The distribution of *Vittaria* and *Trichomanes* gametophytes in Pennsyl-

vania supports the hypothesis of Farrar et al. (1983) that the post-Pleistocene dispersal of *Vittaria* gametophytes has been very limited, probably to spread of gemmae, whereas that of *Trichomanes* may have involved a northern extension of sporophytes. However, Farrar (1985) demonstrated that the independent gametophytes of both *Vittaria* and *Trichomanes* are enzymatically distinct from sporophyte-bearing species of their respective genera now living in the continental United States.

In summary, *Vittaria* gametophytes are quite rare in Pennsylvania, being known from only 24 sites primarily in unglaciated areas. The five new stations in glaciated country are all close to the Wisconsinan terminal moraines which probably parallel the northern range limits of this taxon. *Trichomanes* is more widespread, including numerous stations in glaciated regions, and will probably be found at many more sites.

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# THE REDISCOVERY OF THE GLOBALLY ENDANGERED CLOVER, *TRIFOLIUM STOLONIFERUM*, IN INDIANA

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AND ELLEN M. JACQUART

## ABSTRACT

Two populations of the globally endangered running buffalo clover (*Trifolium stoloniferum*) were recently discovered in Ohio County in southeastern Indiana. The habitats of the populations are limestone gravel wash, mesic upland forest, and mesic floodplain forest. All of the sites are grazed to various degrees by cattle. Absence of the clover in similar but ungrazed sites adjacent to the populations suggests that effects of grazing are beneficial. Suppression of competing understory vegetation is likely the most beneficial effect. The endangered status of *T. stoloniferum* probably reflects actual rarity, but misconceptions by botanists of the clover's morphology and habitat may account for the extreme paucity of recent collections. Recommendations for field survey techniques are given.

Key Words: *Trifolium stoloniferum*, endangered species, habitat, Indiana

## INTRODUCTION

Since the publication by Brooks (1983) on the status of running buffalo clover (*Trifolium stoloniferum* Muhl. ex Eaton) and listing of the clover as a federally endangered species [Federal Register 52(108): 21478. June 5, 1987], a great deal of interest has been generated among botanists to locate populations of this rare native legume. The clover, a primarily midwestern species ranging from West Virginia to Kansas, has, for reasons unknown, seemingly disappeared. At the time of listing, only two extant populations were known, both in West Virginia (Bartgis, 1985). At this writing there are five known populations: two in West Virginia, two in Indiana, and one in Kentucky (Jacobs, 1987).

Indiana botanists were unaware until recently of any records of *Trifolium stoloniferum* for the state. The main reason for this ignorance is the absence of *T. stoloniferum* specimens in Indiana herbaria, and exclusion of the clover from the state's major floristic work, *Flora of Indiana* (Deam, 1940). We first learned of the clover's occurrence in Indiana from Brooks' (1983) paper, where three pre-1900 collections from Clark, Delaware, and Marion Counties were cited. The collections are housed in eastern U.S. herbaria, and as is true with most old collections, their labels lack suitable information for use in re-locating specific collecting

sites. What was useful to our re-location efforts however, was an 1816 diary entry by the early explorer and botanist David Thomas, who, while traveling through southeastern Indiana near the Ohio County community of Rising Sun, noted: "The buffalo, or wild clover, grows abundantly among the bushes, on the fertile though narrow flats of a small brook, down which the road winds. It appears to vegetate earlier than the white clover; or at least, the seed is sooner ripe" (Thomas, 1916). This description of the habitat (of what was apparently *T. stoloniferum*), along with the location information, proved to be significant to our search. On June 16, 1987, while surveying streambank terraces (narrow flats) in the hills near Rising Sun, possibly not far from Thomas' observation of the "wild clover," we located two populations of *T. stoloniferum.*

## HABITAT

The two Indiana populations were discovered growing in and along two small tributaries approximately 2.5 km apart and within 3.0–5.5 km of the Ohio River. This area is similar to the adjacent Bluegrass region of Kentucky, so much so that Homoya et al. (1985) identified it as the Bluegrass Natural Region (of Indiana). The topography of this natural region, although glaciated, is surprisingly rugged, especially in the Switzerland Hills section where the clover occurs. Although cliffs are rare, bedrock composed of Ordovician limestone is evident, mainly as gravel and slabs in streambeds and on steep, eroding slopes. Most of the soil series present in the region are neutral to alkaline. The major native vegetation type is mesic deciduous forest, with American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), white ash (*Fraxinus americana* L.), chinquapin oak (*Quercus muhlenbergii* Engelm.), red oak (*Q. rubra* L.), blue ash (*Fraxinus quadrangulata* Michx.), American basswood (*Tilia americana* L.), Ohio buckeye (*Aesculus glabra* Willd.), and tulip tree (*Liriodendron tulipifera* L.) as typical dominants.

Running buffalo clover occurs in three specific habitat types: 1) narrow, mesic floodplain forest; 2) steep, mesic upland forest; 3) gravel wash located in small, high-gradient, ephemeral streams. The greatest number of individuals, occurring in five scattered colonies (one to thirty plants each), is situated on the lower slopes of the hills and on floodplain terraces that border the two pre-

viously mentioned tributaries. The sites are quite mesic, consisting of relatively rich, neutral, Eden flaggy silty clay loam (Nickell, 1981). Although the sites are forested, their understory is rather open due to the selective removal of vegetation by cattle grazing. Grazing intensity ranges from light to heavy, with the greatest number of *Trifolium stoloniferum* plants in the moderately grazed sites. Adjacent areas with similar environmental conditions, but without grazing (cattle are excluded by a fence), do not have the clover.

Although most of the lower canopy species have been reduced or removed by the grazing, the mid- and upper canopy species are still intact. These species include American sycamore (*Platanus occidentalis* L.), box elder (*Acer negundo* L.), red elm (*Ulmus rubra* Muhl.), Ohio buckeye (*Aesculus glabra* Willd.), pawpaw (*Asimina triloba* (L.) Dunal), and spicebush (*Lindera benzoin* (L.) Blume). Herbaceous associates of *Trifolium* include *Cryptotaenia canadensis* (L.) DC., *Carex jamesii* Schwein., *Pilea pumila* (L.) Gray, *Laportea canadensis* (L.) Weddell, *Leersia virginica* Willd., *Poa compressa* L., *Verbesina alternifolia* (L.) Britt., *Eupatorium rugosum* Houtt., *Alliaria petiolata* (Bieb.) Cavara and Grande, *Polemonium reptans* L., *Podophyllum peltatum* L., *Polygonum hydropiperoides* Michx., *P. punctatum* Ell., and *P. virginianum* L.

The gravel wash sites, where three *Trifolium stoloniferum* colonies occur, consist of slightly elevated, rocky bars and narrow braids of Ordovician limestone gravel and slabs. Although plants in the gravel wash are sometimes damaged by occasional high stream flow, the scouring action prevents establishment of woody species and consequently exposes the clover to light intensities higher than are normally found in undisturbed mesic forest environments. These higher light intensities may be an important factor in perpetuating the clover in areas that otherwise are too shaded to supply the critical light needs of the clover (see later discussion). Species associates of the clover in the gravel wash include *Pilea pumila, Leersia virginica, Eupatorium rugosum, Polygonum hydropiperoides, Lysimachia nummularia* L., *Trifolium repens* L., *T. hybridum* L., *Taraxacum officinale* Weber, *Acalypha rhomboidea* Raf., and *Festuca elatior* L.

## COMMENTS ON REASON FOR RARITY

One reason for the decline of *Trifolium stoloniferum,* as suggested by Bartgis (1985), has been the elimination from the clo-

ver's range of bison and their attendant disturbances. The implication is that the clover's requirements are uniquely tied to bison, and as bison disappeared, so did the clover. Although we do not question the former importance of bison in the clover's ecology, we suggest that it is not any inherent quality of bison that is critical, but rather, the removal or suppression of competing vegetation, regardless of the agent responsible. Supporting this contention is the fact that all known extant populations of the clover occur either along trail openings or in sites grazed by livestock or infrequently mowed (Bartgis, 1985; Jacobs, 1987). We suspect that without removal or suppression of competing vegetation, a site becomes too shaded, especially in mesic forest communities, to satisfy minimum light needs of the clover. Therefore, communities that are not maintained to suppress competing vegetation are generally unsuitable for *T. stoloniferum.* This observation thus explains the clover's absence in ungrazed sites immediately adjacent to existing populations in Indiana.

Grazing by exotic livestock, at least to a certain degree, can evidently establish and maintain *Trifolium stoloniferum* habitat. Given this, how can it be that the clover has declined, as there appears to be no time in our history when grazing, either by bison or livestock, has not been common? At this time the question cannot be adequately answered. Several other suggested causes for the decline, including severe landscape alteration, disease, loss of rhizobial associates, fire suppression, competition from exotics, and predation, may all prove to be important (Brooks, 1983; Bartgis, 1985; Davis, 1987; Jacobs and Bartgis, 1987), but more research is obviously needed.

One overlooked factor that may account for the paucity of currently known populations of *Trifolium stoloniferum* is an apparent misconception of the species' habitat. As Brooks (1983) pointed out, and our experience confirms, the clover grows predominantly in moist, well-drained woodland associated with watercourses. It generally does not, as Fernald (1950) and Gleason (1952) stated, occur in dry woodlands and prairies. This confusion may stem from the assumption by botanists (including Fernald and Gleason) that the habitat of *T. stoloniferum* is the same or similar to that of the other buffalo clover, *Trifolium reflexum* L., a plant typically occurring in dry, open sites (that are commonly acid in reaction as well). Not surprisingly then, we have encountered several botanists who have searched for *T. stoloniferum* in

the wrong habitat. Similarly, many botanists avoid forest sites that are grazed, further reducing the possibility of finding the clover.

Another hindrance to field recognition by botanists is the illustration of *Trifolium stoloniferum* in Gleason (1952), which showed two widely spaced leaves on the flowering stem, and gave the impression that the stem is leafy throughout. In fact, the stem is essentially scapose except for two opposite or subopposite leaves that subtend the inflorescence. This distinction was also omitted from the text. Although one can correctly key to *T. stoloniferum* in Gleason, the illustration can give one an incorrect search image for detecting plants in the field.

## RECOMMENDATIONS FOR FIELD SURVEYS

In all likelihood *Trifolium stoloniferum* is indeed a rare species. However, it is probable that the clover exists in several as yet undiscovered sites. Summarizing the information for the purpose of further surveys, the clover should be sought in disturbed mesic forests, particularly those along watercourses that have limestone and/or neutral to alkaline soils. Presence of limestone and/or alkaline soils may reflect a critical habitat requirement for the clover because the majority of the collections throughout its range, excepting those in West Virginia, were made in regions having predominantly alkaline substrates. Ideally, the sites should have an open understory, subject to light to moderate grazing or infrequent mowing. Limestone gravel wash sites, especially those within high-gradient streams, should also be inspected. One should search for a stoloniferous clover that has the appearance of a large, robust *Trifolium repens*. Unlike *T. repens, T. stoloniferum* does not produce a scape at anthesis, but rather an inflorescence subtended by a pair of leaves. In the absence of flowering stems, *T. stoloniferum* can be distinguished from *T. repens* by its green, leafy stipules (1–2 cm long) at the petiole attachment to the stolon. *Trifolium repens* has pale stipules generally less than 1 cm in length.

## ACKNOWLEDGMENTS

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# THE MARSH DANDELION (*TARAXACUM* SECTION *PALUSTRIA*; ASTERACEAE) IN CANADA AND THE ADJACENT UNITED STATES

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## ABSTRACT

*Taraxacum turfosum* (Schultz-Bipont) van Soest, a microspecies of the distinctive Section *Palustria* (*Taraxacum palustre, s. lat.*); Asteraceae, was found to be abundant in eastern Ontario and adjacent areas of Quebec and New York state. Earlier reports of the Section are attributed to other taxa. This report is the first verified occurrence of a species of Section *Palustria* in North America. Its distinctive morphology and habitat are described. The oldest collection of *T. turfosum* is from 1964, suggesting a recent introduction for this European taxon. Mechanical transport by high speed road traffic, snow plows and grass mowers is apparently assisting its rapid spread along roadways. Viable seed is produced and is likely wind dispersed. Evidence of declining populations was observed following two dry winter/early spring seasons in eastern Ontario.

Key Words: *Taraxacum turfosum, Taraxacum* Section *Palustria,* Asteraceae, distribution, dispersal, halophytes, Ontario, Quebec, New York

## INTRODUCTION

*Taraxacum* is an extremely complex genus of mostly apomictic herbs; there are over 1200 proposed European species (over 130 in Great Britain alone; Clapham et al., 1987). Large numbers of these microspecies have been randomly introduced into temperate North America; Boivin (1972) noted over 100 in Canada alone. Most North American manuals take a cautious view of the group, submerging the many microspecies into a few broadly defined taxa. Even then, there is little consensus. Gleason (1968) cited three species in eastern North America while Fernald (1950) noted 11 for the same area and Scoggan (1979) had that number for all of Canada. Faced with this perplexing situation many North American manuals treat all introduced *Taraxacum* under *T. officinale* Weber (e.g., Scoggan, 1957; Roland and Smith, 1969; Boivin, 1972).

Major European floras subdivide *Taraxacum* into a number of Sections and groups; 21 Sections are recognized in Flora Europaea (Richards and Sell, 1976). Although the limits of some of these Sections are not always clear, the approach is a practical one for areas with many microspecies.

In 1983 Karen L. McIntosh and I collected a strikingly different *Taraxacum* near Ottawa, Ontario which we identified as a member of the Section *Palustria* Dahlst. This taxon is often treated as *T. palustre* (Lyons) DC., *s. lat.* European *Taraxacum* authority A. J. Richards confirmed our *Palustria* identification on a series of collections, referring them to *T. turfosum* (Schultz-Bipont) van Soest, ". . . a widespread species from Central Europe, particularly the north side of the Alps" (A. J. Richards, pers. comm.). He further advised that ". . . this constitutes the first record for Section *Palustria* . . . outside of Europe (except Turkey)." While *T. palustre* is listed in North American sources (Fernald, 1950; Kartesz and Kartesz, 1980), this listing is apparently based on misidentified specimens (probably Sections *Taraxacum* Dahlst. and *Spectabilia* Dahlst.).

In this study I have attempted to delineate the Canadian range of *Taraxacum turfosum* (and therefore, Section *Palustria*), as well as to consider major ecological, distributional, and identification characteristics of Section *Palustria.*

## METHODS

The collections of introduced *Taraxacum* in DAO, CAN, and TRT, some of which had been previously examined by A. J. Richards, were reviewed for records of *T. turfosum* or other *Palustria* microspecies. This examination also included a sheet labelled *T. palustre* in NYS. Searches of suitable habitat were conducted along major roads over much of eastern Ontario and parts of adjacent Quebec and New York state in the spring seasons of 1984 to 1988. Vouchers have been deposited in various public herbaria including DAO, TRT, CAN, MICH, NYS, and in my private collection. (A list of representative specimens is on file with CISTI.)

## IDENTIFICATION

*Taraxacum* Section *Palustria* is not difficult to identify. A variety of features based on plants verified by A. J. Richards and apparent from his major *Taraxacum* studies (Richards, 1972; Richards and Sell, 1976) are used in the following description.

*Taraxacum turfosum* is often the first *Taraxacum* to bloom in southern Ontario and Quebec; I have recorded flowering dates

from April 23 to May 29. It grows in wet or flooded sites in calcareous gravel or clay over limestone or marble bedrock. It thrives in seasonally flooded highway ditches where a variety of weedy halophytic vascular plants are common. These sites develop highly salt-rich substrates from dissolved winter road deicing chemicals (Reznicek et al., 1976; Catling and McKay, 1980). Figure 1 illustrates the erect, narrow, remotely serrate leaves which are strikingly different from the deeply cut and reflexed leaves of most introduced *Taraxacum* taxa in North America. The diagnostic very dark, broad, strongly appressed exterior involucral bracts (even with mature fruit) are also indicated in Figure 1 (cf. Richards, 1972; Clapham et al., 1987). Only the related Section *Spectabilia* is readily confused in North America with *Palustria.* I have seen *Spectabilia* specimens in Ontario and New York state growing singly or in small numbers in moist sites, though not as wet as those of *Palustria. Spectabilia* has broad exterior involucral bracts like *Palustria* but they are reflexed, even in the flowering stage. *Spectabilia* leaves are more deeply cut (to the midrib in some taxa), the plants are larger overall, and they flower later than *Palustria* taxa by a few weeks (pers. obs.). The vivid purple color of major veins along the underside of the leaves is a conspicuous character of taxa of Section *Spectabilia* (Clapham et al., 1987).

## DISTRIBUTION

*Taraxacum turfosum* is locally abundant across eastern Ontario but remains rare west of Kingston despite the abundance of wet, salt-rich ditch habitat in which many associated halophytes are common (Reznicek et al., 1976). While acid substrates, like the broad band of acidic sand west of Hawkesbury, Ontario, create barriers to its spread, its small population west along Highway 401 where no barriers are evident suggests that *T. turfosum* is just reaching that area and will become more common in the future.

The oldest record of *Taraxacum turfosum* seen in this study is the 1964 collection from Lake Simcoe (Sibbalds Point Provincial Park, York Regional Municipality, Ontario; May 9, 1964, *M. G. Dumais 552* (TRT)). Ironically, this specimen is the most isolated record in Ontario of *T. turfosum* and was one of only six found in public herbaria. The site is adjacent to a discontinuous band

Figure 1. Single plant of *Taraxacum turfosum* (Section *Palustria*); note erect, lanceolate, unlobed leaves and dark, wide, appressed exterior involucral bracts (Norfolk, St. Lawrence Co., New York, May 15, 1988).

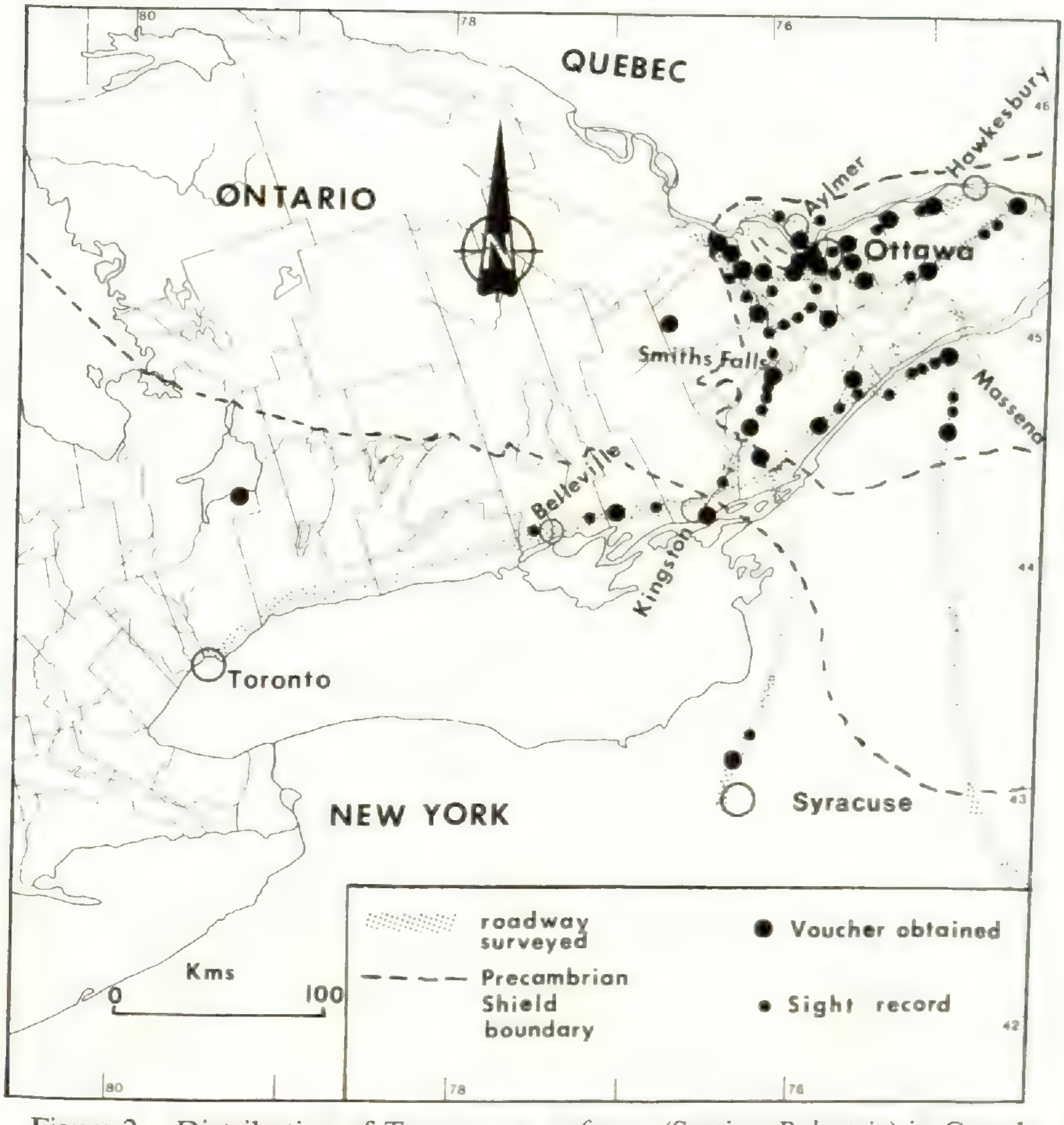


Figure 2. Distribution of *Taraxacum turfosum* (Section *Palustria*) in Canada and the adjacent United States.

of limestone plain that extends across the southern edge of the Precambrian Shield in Ontario (Chapman and Putnam, 1966); *T. turfosum* will likely be found more widely in this band.

Mitchell (1986) reported *T. palustre* as a rare introduction for New York state based on a 1927 collection from the Albany area. I have revised that specimen to Section *Spectabilia*. The records from this study, therefore, represent the first records of Section *Palustria* for New York and, apparently, the United States.

## DISPERSAL

Ontario populations of *Taraxacum turfosum* produce viable seed, as indicated by the plant which grew up in my yard 10 m

from a plot where *T. turfosum* had been producing seed for three years. The habitat between the two sites was unsuitable, suggesting that the seed was carried from the established plot. The Minnow Lake station in Lanark County, Ontario (west of Smiths Falls; *see* Figure 2) offers evidence for wind dispersal of the seed. The site is in an area of marble substrate surrounded by kilometers of unsuitable acidic substrate and can be reached only on foot or by four-wheel-drive vehicle.

Mechanical transportation of seed, whole plants, and other reproductive parts by snow plows, high speed vehicles, and construction activities along roadways has been cited as a likely aid in the spread of other salt tolerant aliens (Reznicek et al., 1976; Catling and McKay, 1980; Reznicek, 1980; Brunton and Catling, 1981; Stuckey, 1981). The activity of grass mowers along roadside ditch sites of *Taraxacum turfosum* may be particularly useful in transporting the seed of this species.

*Taraxacum turfosum* was particularly abundant in the Ottawa, Ontario area in the 1984–86 period and appeared to be increasing throughout this time. Little or no spread was noted in the following dry winter/early spring seasons of 1986/87 and 1987/88. Sites where I knew *T. turfosum* to be common 1984–86 supported no plants in 1987 and 1988. Such sites were dominated by other *Taraxacum* taxa (usually Sections *Vulgaria* Dahlst. or *Spectabilia* taxa) in the now drier habitat.

## ACKNOWLEDGMENTS

I thank my wife, Karen McIntosh, for her important field assistance throughout the study. A. J. Richards of the University of Newcastle Upon Tyne, England provided invaluable determinations and important information. I also appreciate the access to material held in the CAN, TRT, and DAO herbaria granted by their respective curators. Other valuable assistance was offered by D. J. White of Macdonald's Corners, Ontario, C. J. Sheviak, New York State Museum, Albany, and J. McNeill, Royal Botanical Garden, Edinburgh, Scotland. An earlier draft of the manuscript also benefitted significantly from the constructive criticisms offered by John C. Semple, an anonymous reviewer, and the editor.

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# NEW ENGLAND NOTE

# DISCOVERY OF *SPOROBOLUS ASPER* (POACEAE) IN MAINE

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On September 26, 1984, we discovered a small population of *Sporobolus asper* (Michx.) Kunth at a botanically diverse riverbank of the Aroostook River in Wade, Aroostook County, Maine. The species was not mentioned in Richards et al. (1983), and no prior Maine collection records of it were found at NEBC and MAINE. This population thus represents the first for the species in Maine.

*Sporobolus asper* was growing in stony alluvium and bedrock crevices within prairie-like vegetation of short, native graminoids along a series of flood-scoured bedrock ledges at 46°46′N, 68°12′W, and at an elevation of 140 m. The vegetation was dominated by the low, mat-forming grass, *Muhlenbergia richardsonis* (Trin.) Rydb. Other associates were *Scirpus clintonii* Gray, *Scirpus cespitosus* L., *Allium schoenoprasum* L. var. *sibiricum* (L.) Hartman, *Potentilla fruticosa* L., *Potentilla arguta* Pursh, *Deschampsia cespitosa* (L.) Beauv., *Spartina pectinata* Link, *Muhlenbergia glomerata* (Willd.) Trin., *Rosa blanda* Ait., *Prunus pumila* L. var. *depressa* (Pursh) Gleason, *Campanula rotundifolia* L., and *Lobelia kalmii* L.

*Sporobolus asper* was not included in a list of New England rare and endangered plants (Crow et al., 1981), but nevertheless might be regarded as a rarity throughout New England. The species is extant at a single Vermont station (*Zika 7770,* VT), and is considered endangered in this state (Everett Marshall, pers. comm.). The species is not known to be extant in Massachusetts (Bruce Sorrie, pers. comm.), Connecticut (Les Mehrhoff and Ron Rozsa, pers. comm.), and Rhode Island (Richard Enser, pers. comm.). Collection records indicate a historic distribution of 10 towns in Massachusetts (NEBC, GH), 17 towns in Connecticut (NEBC, GH, CONN), and three towns in Rhode Island (NEBC, GH). *Sporobolus asper* has not been reported from New Hampshire.

In New Brunswick, Canada, *Sporobolus asper* was considered

rare (Hinds, 1983), and is now thought to be extirpated (Harold Hinds, pers. comm.). In New York State, distribution records of this species on file at the New York State Museum show 46 different collection sites, most of them from the eastern part of the state. *Sporobolus asper* is not considered rare in New York (Steve Clemants, pers. comm.).

*Sporobolus asper* has been ranked S1 (state endangered) by the Maine Natural Heritage Program (Amy Forrester, pers. comm.). The Wade specimen is deposited at NEBC (*Rawinski, Rasmussen & Rooney 2179,* NEBC).

## ACKNOWLEDGMENTS

For providing information on the current status of *Sporobolus asper,* we thank Everett Marshall, Hal Hinds, Amy Forrester, Bruce Sorrie, Rick Enser, Les Mehrhoff, Ron Rozsa, Bob Zaremba, and Steve Clemants. We are grateful to The Nature Conservancy (USA) for providing financial support toward this field work.

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RHODORA, Vol. 91, No. 866, p. 222, 1989

# BOOK REVIEW

D. Dudley Williams. 1987. *The Ecology of Temporary Waters.* Pp. vii + 205; 57 figs. and illus. Croom Helm, London. Available from Timber Press, 9999 S.W. Wilshire, Portland, OR 97225. (Hardbound $36.95)

Here is a book on an unusual topic but one that will certainly prove to be thought-provoking. Written by a Professor of Zoology at the University of Toronto, it has a mass of material not easily available to ecologists, limnologists, botanists, and zoologists, especially those concerned with plant–animal adaptation.

Temporary waters are defined as natural bodies of water in many parts of the world that experience a dry season and how this variation between humidity and drought affects plant and animal life that has become adapted to the variation. It is a novel treatment of a very basic subject and, as such, deserves wide attention, especially in north temperate regions.

The nine chapters treat 1) Introduction to Temporary Waters; 2) Factors Governing Formation of Temporary Waters; 3) Abiotic Features of Temporary Waters; 4) Biota; 5) Special Adaptations; 6) Colonization Patterns; 7) Other Temporary Water Habitats; 8) Applied Aspects of Temporary Waters; 9) Temporary Water as Study Habitats.

Since temporary waters vary all the way from water in hollow tree trunks and pitcher plants to seasonal ponds and waterways, they are of very specific ecological significance. Little is available on this subject and Professor Williams is to be congratulated in making easily available the contents of this new book.

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RHODORA, Vol. 91, No. 866, p. 223, 1989

# BOOK REVIEW

Jones, Samuel B. and Nancy Coile. 1988. *The Distribution of the Vascular Flora of Georgia.* Address inquiries to: Herbarium, Department of Botany, University of Georgia, Athens, GA 30602. ($3.00)

*The Distribution of the Vascular Flora of Georgia* by Samuel Jones and Nancy Coile, in the words of the authors, "serves as an official checklist of the flora of the state of Georgia based upon voucher specimens deposited in institutional herbaria."

Since we do not have a manual of the flora of Georgia or of the Southeast, this book will be useful to plant systematists and ecologists who use *The Manual of the Vascular Flora of the Carolinas* by Radford, Ahles, and Bell in their courses and research. It will also be useful to persons who deal with the identification and protection of rare and endangered species in Georgia.

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The New England Botanical Club is a non-profit organization that promotes the study of plants of North America, especially the flora of New England and adjacent areas. The Club holds regular meetings, has a large herbarium of New England plants, and a library. It publishes a quarterly journal, RHODORA, which is now in its 90th year and contains about 500 pages a volume.

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# Rhodora

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# RHODORA



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**Cover Illustration**

*Agalinis acuta* Pennell (Sand-Plain Gerardia). A very rare plant of the coastal plain in danger of extinction; known only from Cape Cod and Long Island. Recently listed by the U.S. Fish & Wildlife as Threatened. Original artwork by Tess Feltes; from *New England's Rare, Threatened and Endangered Plants*. Crow, G. E. 1982. Reproduced by permission.

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## A NEW *SPIRANTHES* (ORCHIDACEAE) FROM ASH MEADOWS, NEVADA[1]


CHARLES J. SHEVIAK



### ABSTRACT

*Spiranthes* occupying moist sites in Ash Meadows, Nye County, Nevada, which have been cited as *S. romanzoffiana* Cham., are described as the new species *S. infernalis* Sheviak. This species is distinguished by very small flowers with free perianth segments spreading at the apices, the segments ochraceous-ochroleucous with fleshy, emerald-green bases, and lips broadest near the middle.



Key Words: *Spiranthes infernalis, S. romanzoffiana, S. porrifolia,* Ash Meadows, Nevada


### INTRODUCTION

Ash Meadows, in southern Nye County, Nevada, is famous as a center of endemism of both plants and animals. Lying on the east side of the Amargosa Valley and separated from Death Valley to the west by the Funeral Mountains and the Amargosa Range, the area owes its remarkable biota to a number of carbonate-rich springs which maintain isolated wetland communities scattered across 16,000 hectares of desert now occupying the bed of a Plio-Pleistocene lake (Beatley, 1976; Riggs, 1984; Schwartz, 1984).

The boreal, cool-montane, and alpine *Spiranthes romanzoffiana* Cham. was reported from Ash Meadows by Beatley (1976), based on a single collection from each of two sites. In conjunction with a study of the *S. romanzoffiana* complex, I examined the specimens cited by Beatley and found the plants to be quite distinctive and, although related to *S. romanzoffiana,* well outside

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[1] Contribution #585 of the New York State Science Service.

the known variation in this species. An extensive search of herbaria located throughout the region disclosed only one additional collection of the plant, again from Ash Meadows. In 1985 I visited Ash Meadows and located the plant at a fourth site. Although at the time of my collection the plants had already senesced following seed dispersal, two live plants were collected and have been grown since then in a controlled environment chamber. These bloomed in two subsequent years and have proven to be even more distinctive than was apparent in the pressed specimens. The unique features expressed in these plants warrant recognition as a distinct species:

**Spiranthes infernalis** Sheviak, *sp. nov.* (Figure 1)

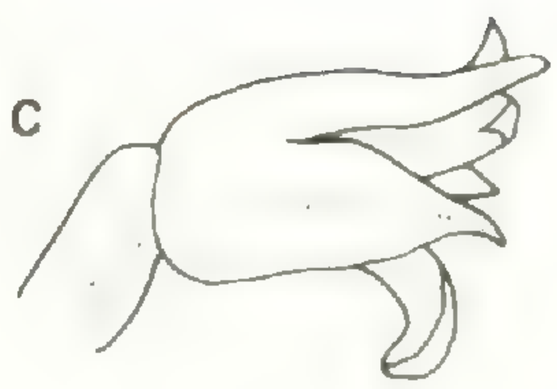
Herba erecta glabra, inflorescentia plerumque minute farinosa. Radices tuberoso-incrassatae. Folia linearia, lineari-lanceolata, vel lineari-oblanceolata, radicalia et saepe cauli versus basim inserta, abrupte bracteis sursum reposita, sub anthesi persistentia. Spica saepissime densissima, 50–130 mm longa, 6–10 mm diametro. Flores 4–6 mm longi, ochroleuci et leviter ochracei, prope bases smaragdini, labelli parte centrali armeniaca. Sepala ad basim connata, apicibus discretis. Labellum 5–6 mm longum, ellipticum, basi constrictionibus abrupte angustata, apicem versus supra minute sed conspicue puberulum.

Herb, slender to stout, 185–390 mm tall, glabrous, commonly minutely and sparsely farinose in the inflorescence. Roots tuberously thickened, to 15 mm in diameter. Leaves persisting into anthesis, linear to linear-lanceolate or linear-oblanceolate, the larger to 150 mm long and 9 mm wide, basal and often extending along the basal half of the stem, the transition to sheathing bracts abrupt. Spike usually very dense, rarely lax, 50–130 mm long, 6–10 mm in diameter. Floral bracts acuminate, the lower 10–20 mm long. Flowers tubular, perianth 4–6 mm long, ochroleucous and slightly ochraceous, with basal ¼ of sepals and petals and up to ½ of lip green and fleshy, remainder of lip ochraceous-ochro-

Figure 1. *Spiranthes infernalis* Sheviak. Drawings from the type collection (a–d: Holotype, *Sheviak 2741a* [NYS]; e, f: Isotype, *Sheviak 2741b* [NYS]). **a, b:** Drawings from photographs of live plant before pressing. **a.** Habit; **b.** Inflorescence. **c–f:** Camera lucida drawings of liquid-preserved flowers. **c.** Flower, lateral view; **d.** Lip, flattened; **e.** Column, lateral view; **f.** Column, ventral view. →

10 cm
a

b
1 cm


c

d
5 mm

e

f
3 mm

leucous and variably orange centrally. Sepals connate basally, lanceolate, acute, the apices spreading. Petals for most of their length associated with the dorsal sepal, lanceolate, obtuse, the apices spreading. Lip 5–6 mm long, broadly (in type) or occasionally narrowly elliptical, often divided by more or less evident constrictions into abruptly narrowed apical and basal segments notably narrower than the middle, the apical segment minutely but conspicuously puberulent above. Scent faint, rose-like.

Chromosome number: $2n = 44$.

TYPE. U.S.A.: Nevada, Nye County: Marshy meadow along stream, in sod of *Distichlis spicata* var. *gracilis,* w/ *Spartina gracilis* and *Anemopsis californica.* W. side of road N.E. from Death Valley Junction, 2.4 mi. S. of turn-off to Devil's Hole, Ash Meadows. Center E. edge Sec. 23, T18S, R50E, elev. 2190 ft. Collected 1984 (*2650*); bloomed in hort. 1985. *C. J. Sheviak 2741a* (HOLOTYPE: NYS).

PARATYPES. U.S.A.: Nevada. Nye County: Same locality as type, 8 August 1984, *C. J. Sheviak 2650* (NYS); Carex-Juncus vegetation type, Ash Meadows, near Crystal Pool, elev. 2190 ft., Sec. 3, T18S, R50E, 4 July 1968, *J. L. Reveal 1488* (CAS *ex* DS, RENO, US); Occas., edge of Ash woods, bank of stream running through large spring-fed area N.W. of Devil's Hole, Sec. 35, T17S, R50E, Ash Meadows, elev. 2200 ft., 14 July 1969, *J. Beatley s.n.* (US); In alkali meadow at Collins Ranch, with *Fraxinus velutina* var. *coriacea, Mentzelia leucophylla,* and *Oxystylis,* Ash Meadows, elevation ca. 2200 ft., 20 June 1980, *S. A. Cochrane & T. A. Swearingen 1577* (UNLV).

ETYMOLOGY. "Of the netherworld" or "of the lower regions," in allusion to the physiography and extraordinarily hot climate of the species' habitat and in keeping with the local penchant for names that reflect these conditions.

*Spiranthes infernalis* belongs to a small group of species including *S. romanzoffiana* and *S. porrifolia* Lindl. These species have in common sepals basally connate and forming a tube, lips with a very narrow subapical constriction, and chromosome numbers based on 22. Of these three species, *S. romanzoffiana* is distinct in its white, rather urceolate flower, its base broad, appearing somewhat inflated (I have heard the flower described as looking like it had swallowed a pea); strongly pandurate lip (the apex beyond the constriction broadly dilated); and sepals and petals united to form a hood above the lip. In both *S. porrifolia*

and *S. infernalis,* the flowers are ochroleucous with the sepals and petals free at the apices, these spreading or, in *S. porrifolia,* often recurving. The lips of these species (Figure 2) lack the marked apical dilation of *S. romanzoffiana,* but vestiges of a pandurate form are evident in the common presence of a subapical constriction and variably expanded apical margin, especially in *S. porrifolia.* In *S. infernalis,* after the flower has been open only a few days, this tissue of the apical margin commonly dies, drying as a darker irregular involute mass adherent to the surface of the lip and emphasizing the differentiation of the apical segment. The width and general shape of the lip in *S. infernalis* and *S. porrifolia* is somewhat variable, these species exhibiting similar patterns of variation from broadly to narrowly elliptical in *S. infernalis* and, in *S. porrifolia,* from ovate to lanceolate. In both *S. infernalis* and *S. porrifolia* the upper surface of the apical segment bears a variably dense cushion of peg-shaped trichomes (these appearing ligulate in dried material), a most distinctive feature lacking in *S. romanzoffiana.* The flowers of *S. infernalis* are much smaller (4–6 mm long) than those of *S. romanzoffiana* and *S. porrifolia* (typically 8–12.5 mm long). They have the proportions of those of *S. romanzoffiana,* being rather broad-based and robust, whereas those of *S. porrifolia* are much more slender, without the inflated base (Figure 3). In *S. romanzoffiana* a certain grace is imparted by the geometric precision of the flower's curving hood and downward-curving lip and the rigid ranking of the inflorescence. In *S. porrifolia* and *S. infernalis,* the independently spreading apices of the perianth segments give an aspect to the flowers simply of an open tube, and the geometry of the inflorescence is correspondingly obscured and less elegant. The inflorescence of *S. infernalis* is highly distinctive, the dense arrangement of very small flowers tending to obscure the individual components of the inflorescence and, in some longer inflorescences, suggesting that of a *Plantago.*

The most striking feature of *Spiranthes infernalis* is floral color. As is typical of nearly all species in the genus, flowers of *S. romanzoffiana* are uniformly white or ivory, and those of *S. porrifolia,* ochroleucous. In *S. infernalis,* however, the slightly duller, ochraceous-ochroleucous color evident upon casual observation is limited to the median and apical portions of the sepals and petals and to the more marginal portions of the lip. The basal quarter to half of each segment is deep emerald green, and the

Figure 2. Lips (flattened) of *Spiranthes infernalis* Sheviak (Aa–Aj) and *S. porrifolia* Lindl. (Ba–Eg). Camera lucida drawings from liquid-preserved material (Aa, Ac, Bc) and pressed herbarium specimens.

*Spiranthes infernalis*: NEVADA: Nye County. **Aa.** *Sheviak 2741a* (NYS) (Holotype); **Ab.** *Sheviak 2650b* (NYS) (collected in field); **Ac.** *Sheviak 2741b* (NYS) (Isotype; same plant as in "Ab," under cultivation). **Ad–Af:** *Cochrane & Swearingen 1577* (UNLV). **Ad.** Plant *1*; **Ae.** Plant *2*; **Af.** Plant *3*. **Ag–Aj:** *Reveal 1488* (DS). **Ag.** Plant *1*; **Ah.** Plant *2*; **Ai.** Plant *3*; **Aj.** Plant *4*.

*Spiranthes porrifolia*: Population samples from two sites in CALIFORNIA: **Ba–Ca:** El Dorado County. *Sheviak 2510* (NYS). **Ba.** Plant *a*; **Bb.** Plant *b*, collected in

apex and central portion of the lip is pale orange. Such coloration is unknown elsewhere in *Spiranthes, sensu stricto.*

The basal coloration of the perianth corresponds to a zone of thick, rigid, fleshy tissue and in the lip is expressed as a basal segment that is markedly narrower than the middle of the lip. The differentiation of this segment is unique in the genus.

*Spiranthes* often exhibit marked phenotypic plasticity in floral characters. Stressed individuals in the field may be small-flowered, but under cultivation often produce larger flowers which may display more clearly any distinctive features (Sheviak, 1973, 1982). Similarly, the upper flowers of an inflorescence frequently are reduced in size and non-distinctive, and recent work has emphasized the use of only the lowest flowers in an inflorescence (Sheviak, 1982; Catling and Catling, 1988). This situation dictates caution in the interpretation of differences in size and shape. In the present case, under cultivation the two plants of *S. infernalis* collected for this study remained essentially constant in floral features over two years and compared favorably with the remnants of flowers remaining on the dehisced capsules present when the plants were originally collected. Several plants of *S. porrifolia* from two sites (El Dorado County, California: *Sheviak 2510,* NYS; Trinity County, California: *Sheviak & Sheviak 2911,* NYS) in cultivation exhibited a tendency toward larger flowers and broader lips (Figure 2, Bb and Bc). These changes only serve to emphasize the differences between the two species.

The similarity between *Spiranthes infernalis* and *S. porrifolia*

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field; **Bc.** Same plant as in "Bb," under cultivation; **Bd.** Plant *c*; **Be.** Plant *d*; **Bf.** Plant *1*; **Bg.** Plant *2*; **Ca.** Plant *3*. **Cb–Cf:** Trinity County. *Sheviak & Sheviak 2911* (NYS). **Cb.** Plant *a*; **Cc.** Plant *b*; **Cd.** Plant *c*; **Ce.** Plant *d*; **Cf.** Plant *2*.

Individual plants from across the range of *S. porrifolia,* arranged in approximate order of increasing distance from Ash Meadows. CALIFORNIA: **Da.** San Bernardino County, *Parish s.n.* (CAS 51703), plant "*5.*" **Db.** Fresno County, *McDonald s.n.* (CAS 111842). **Dc.** Monterey County, *Howell 30632* (CAS). **Dd.** Tuolumne County, *Keck & Heusi 299* (CAS), plant *3*. **De.** San Joaquin County, *Rattan s.n.* (CAS 50143). **Df.** Marin County, *Howell 22212* (CAS). **Dg.** Napa County, *Raven 2399* (CAS), plant *2*. **Ea.** Sonoma County, *Rubtzoff 4641* (CAS), plant *7*. **Eb.** Lake County, *Ripley & Barneby 6903* (CAS), plant *1*. **Ec.** Mendocino County, *Zeile s.n.* (CAS 501075). **Ed.** Butte County, *Heller 10776* (CAS), plant *2*. **Ee.** Humboldt County, *Eastwood & Howell 4728* (CAS), plant *3*. **Ef.** Humboldt County, *Tracy 15667* (CAS), plant *1*. WASHINGTON: **Eg.** Klickitat County, *Suksdorf 11498* (CAS), plant *1*.

a
b
c
g
d
h
e
i
f
j
5 mm

in the reduction and pubescence of the apical segment of the lip, the pattern of variation in lip shape, the free apices of the sepals and petals, and the general ochroleucous floral color, suggest a close relationship between these two species. Indeed, it seems likely that *S. infernalis* evolved from *S. porrifolia* as increasing aridity isolated a small population in Ash Meadows and eliminated *S. porrifolia* from the rest of the region. The small flower and fleshy perianth base of *S. infernalis* are likely responses to the extremely desiccating conditions of extraordinary heat and saline soils which characterize the species' habitat.

*Spiranthes infernalis* occupies variably moist sites associated with springs and spring-fed streams and marshes. At the site at which I found the species, it occurred within a few meters of a small stream in a seasonally moist or wet community in a sod of *Distichilis spicata* var. *stricta* with *Spartina gracilis* and *Anemopsis californica*. Soil was fine-textured with a high salt content. At the time of collection in early August, the site was very dry and the *Anemopsis* were for the most part withered and brown, as were the *Spiranthes*.

## A NOTE ON RARITY

*Spiranthes infernalis* may be endemic to Ash Meadows. Specimens have not been found from other localities despite an intensive herbarium search. The species has been collected at only four stations, and Beatley (1976) reported that the Crystal Pool colony was extirpated immediately after Reveal's collection was made. I was not able to locate the plant in the general area where Beatley made her collection, but I was uncertain of the precise locality and, of course, could easily have missed the plants if they

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Figure 3. Camera lucida drawings of liquid-preserved flowers, lateral view, of *Spiranthes infernalis* Sheviak (a, b) and *S. porrifolia* Lindl. (c–j). Flowers of *S. porrifolia* in "c"–"i" are small flowers from near apices of inflorescences, chosen to illustrate differences between the species at their closest approach in size. Flower in "j" is from near the base of an inflorescence.

*Spiranthes infernalis*. **a, b:** NEVADA: Nye County, *Sheviak 2741* (NYS). **a.** Plant *a* (Holotype); **b.** Plant *b* (Isotype).

*Spiranthes porrifolia*. **c–f:** CALIFORNIA: Trinity County, *Sheviak & Sheviak 2911* (NYS). **c.** Plant *a*; **d.** Plant *c*; **e.** Plant *2*; **f.** Plant *d*. **g–j:** CALIFORNIA: El Dorado County, *Sheviak 2510* (NYS). **g.** Plant *a*; **h.** Plant *b*; **i.** Plant *c*; **j.** Plant *d*.

were in the same condition as those I found further south. Much of the area, however, was seriously disturbed. Again, because of the condition of the plants I found, I cannot judge abundance at the station I located, but the potential habitat was not extensive. Even if the species is more generally distributed than is apparent from collections, its restriction to fragile wetlands which are threatened by regional groundwater depletion suggests that it be considered for Federal endangered species status.

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# OCCURRENCE OF *WITTROCKIELLA PARADOXA* WILLE (CHLOROPHYTA, CLADOPHORACEAE) IN NORTHEASTERN NORTH AMERICA

G. Robin South

## ABSTRACT

*Wittrockiella paradoxa* Wille (Chlorophyta, Cladophoraceae) is reported for the first time from northeastern North America, at Sam Orr Pond, New Brunswick, Canada. Vegetative plants were found from June–August, 1987, and reproductive plants (bearing aplanosporangia) were found in June and July, 1987. They occurred epiphytically on decaying *Spartina* leaves in an oligohaline-mesohaline saltmarsh habitat.

Key Words: *Wittrockiella,* Chlorophyta, new record, New Brunswick, Canada

## INTRODUCTION

*Wittrockiella paradoxa* Wille (1909) is widespread in northwest Europe (Polderman, 1976), where the plants occur as epiphytes or endophytes on or in a variety of halophytes. Printz (1927) reported *W. paradoxa* from North America, but apart from this report, and South's (1981) description of a population from the San Juan Islands on the Pacific Coast of North America, little is known of its distribution in the New World.

In a recent study of the mat-forming micro-algae of a salt marsh in southern New Brunswick, Canada (Tracy and South, 1989), *Wittrockiella paradoxa* proved to be a frequently-occurring taxon; this discovery represents the first reported occurrence of *W. paradoxa* in eastern Canada, and the first in eastern North America since that of Printz (1927).

## RESULTS AND DISCUSSION

Collections of *Wittrockiella paradoxa* were made from Sam Orr Pond, New Brunswick, during 1987. Samples were obtained from two permanent quadrat sites at 8.0 m and 6.9 m above low water mark; the sites are described in Tracy and South (1989). *Wittrockiella paradoxa* occurred in samples collected on May 7th, June 2nd, July 2nd and August 4th, 1987, and were restricted to the upper (8.0 m above low tide) quadrat.

Plants occurred on the mud surface or, preferably, in and on

the tissues of decaying halophytes, especially *Spartina* spp. Associated micro-algae included a variety of crustose and filamentous cyanobacteria, some other Chlorophyceae [*Rhizoclonium riparium* (Roth) Harvey, *Blidingia minima* (Naeg. ex Kuetz.) Klyin], and *Vaucheria* spp. (Tracy and South, 1989). Although plants occurred in most samples from the upper quadrat, they were sparsely distributed.

Sam Orr Pond *Wittrockiella paradoxa* (Figures 1–6) principally occurred as the 'rhizoidal' form (Wille, 1909; Polderman, 1976), the predominant form in European material (Polderman, 1976). Very few 'cladophoroid' plants were observed, in contrast to the predominance of this form described for the population at Sperry Marsh, Washington (South, 1981).

Plants closely resembled the rhizoidal forms described by Polderman (1976) and South (1981). Cells measured 30 (60) – 50 (100) $\mu$m and were light green; elongate cells [tending to the 'cladophoroid' form described in Polderman (1976) and South (1981)] contained a highly reticulate chloroplast with numerous discoid pyrenoids, the rhizoidal cells contained dense chloroplasts and accumulations of storage products. Cells were thick-walled and some possessed elongate rhizoid-like branches that anchored the filaments to the host plant surface (Figure 5). Plants were reproductive in the June and July, 1987, samples and the aplanosporangia closely resembled those described for European material by Polderman (1976). Aplansporangia opened apically (Figure 6), and were either interspersed among the rhizoidal filaments or terminated a branch filament; aplanospores measured 8–10 $\mu$m. No hair cells were observed.

The upper quadrat site at Sam Orr Pond is subject to irregular tidal flooding. Temperature at the mud surface ranged from 6.5°C (May) to 25.5°C (August), and salinity of the surrounding water table ranged from 3.0‰ to 35.0‰, depending upon the most recent tidal flood cycle. These physical parameters seem to be in

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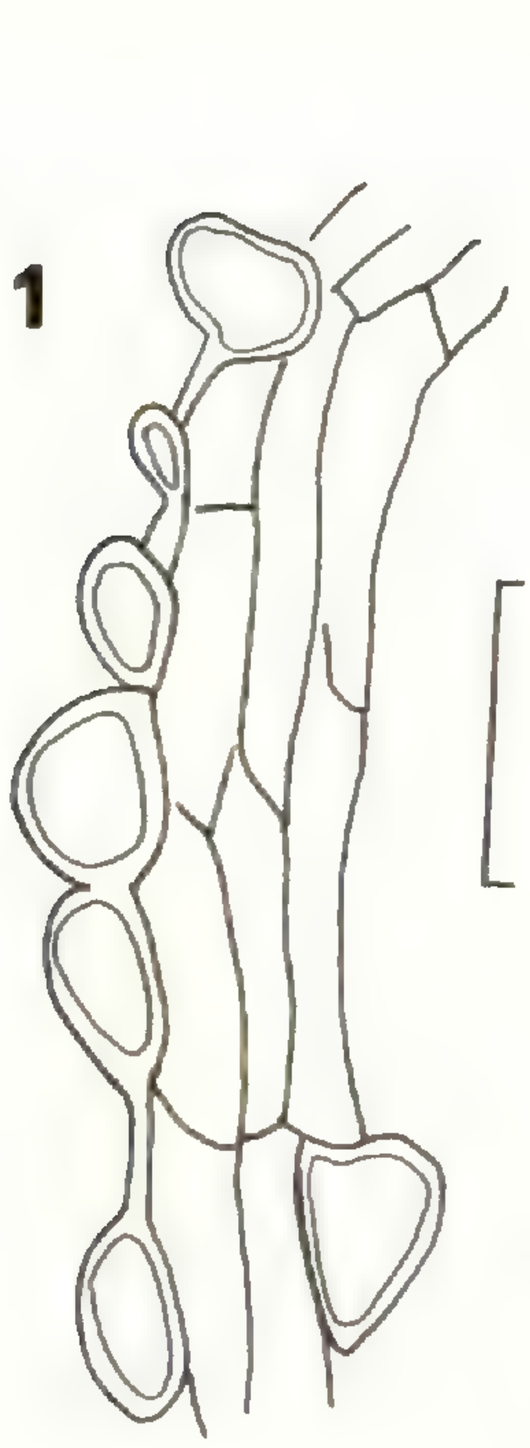
Figures 1–6. 'Rhizoidal' *Wittrockiella paradoxa* from Sam Orr Pond, New Brunswick. **1–3.** Shown 'in situ,' attached to decayed leaf fragments of *Spartina*, August 4, 1987; **4.** August 4, 1987; **5.** June 6, 1987; **6.** June 6, 1987, showing a partially emptied aplanosporangium. Scale bar = 50 $\mu$m.



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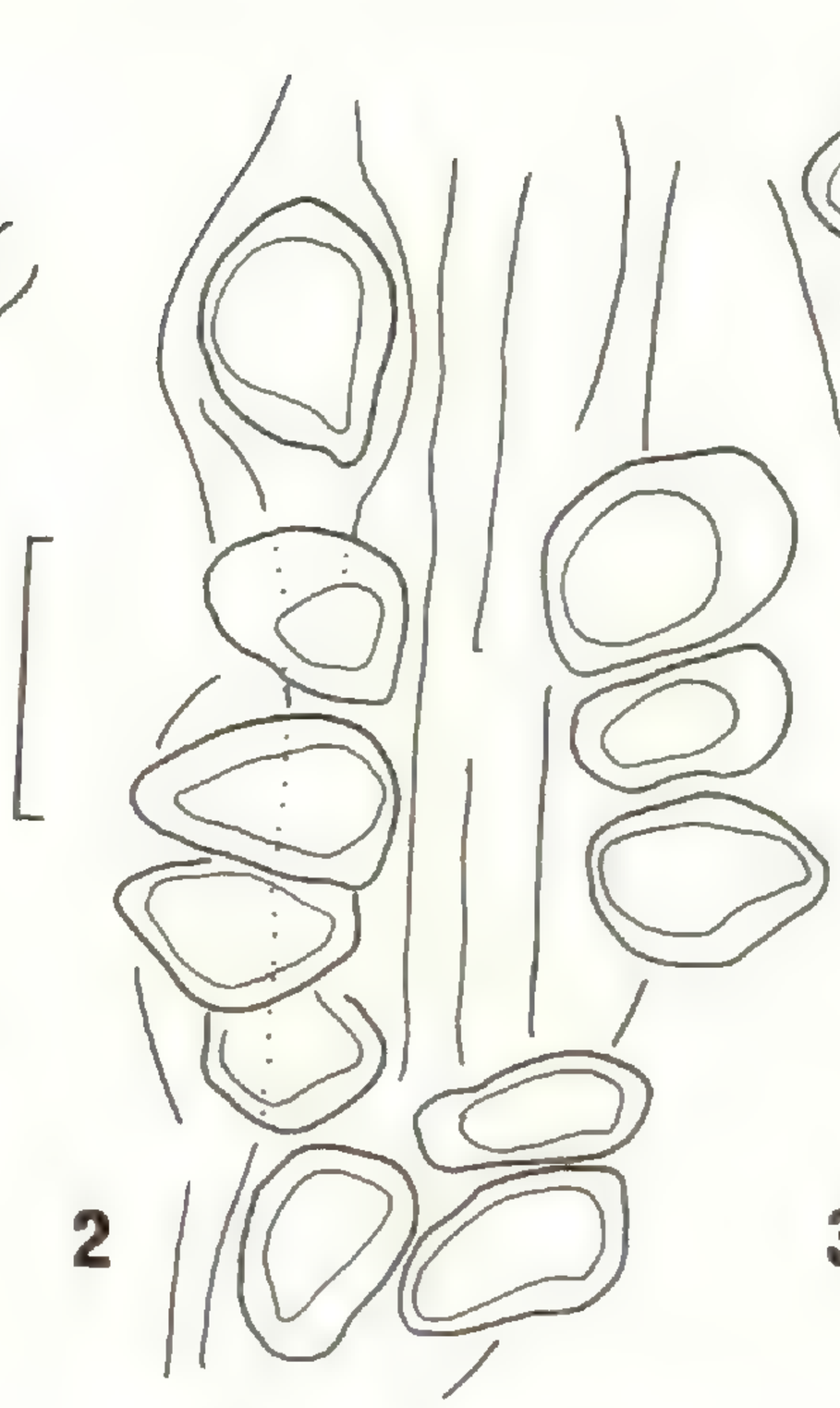

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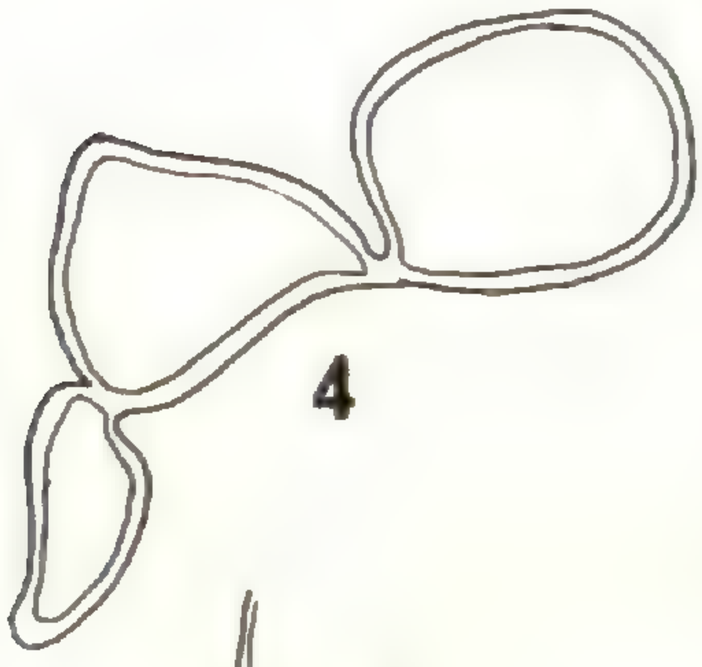

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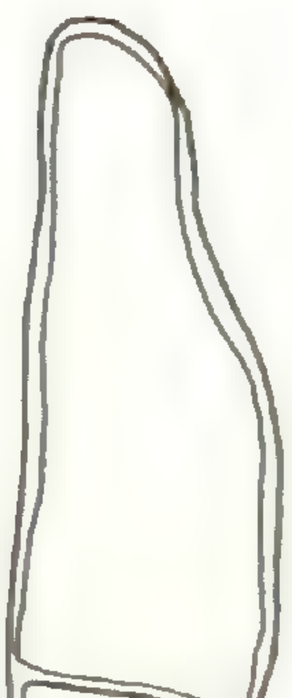

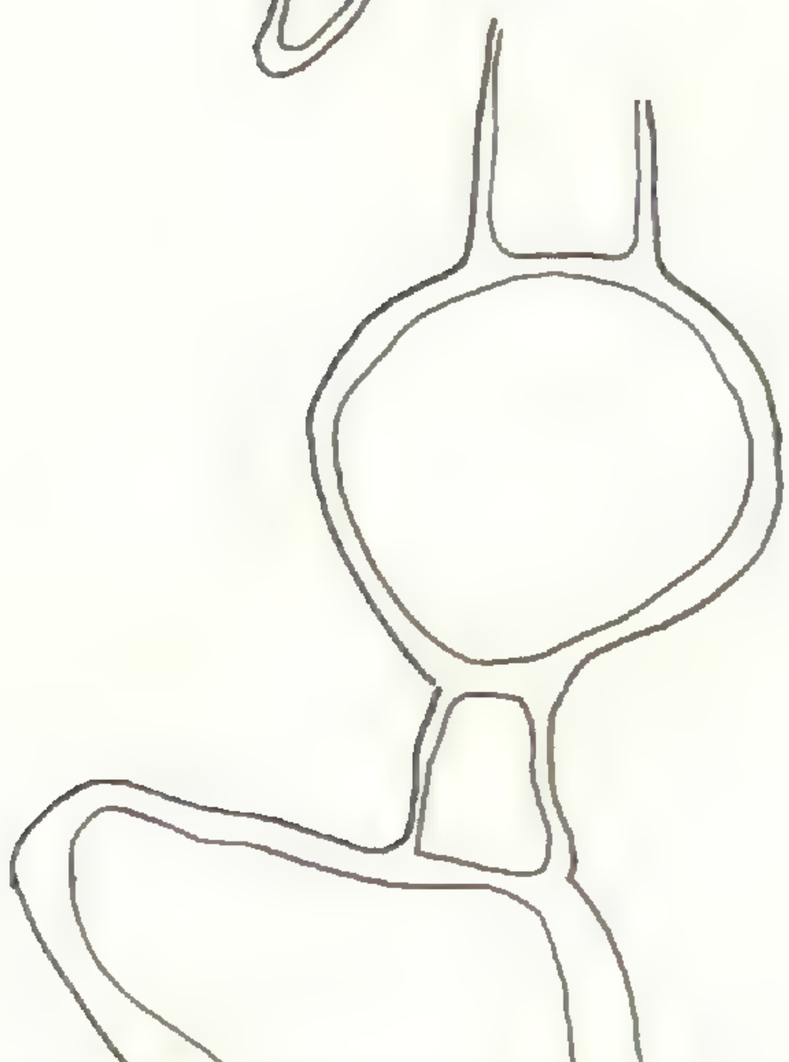

5

6

accord with the oligohaline-mesohaline habitats described for the species in northwest Europe (Polderman, 1976).

It is likely that *Wittrockiella paradoxa* is more widespread than presently reported (South, 1981). The record from Printz (1927) is not well documented, and there are no subsequent records from eastern North America. Its cryptic habitat and possible confusion with other filamentous algae (e.g., *Vaucheria*) make its detection difficult, but it is surprising that *W. paradoxa* has not been reported in previous studies of northeastern North American salt-marshes.

## ACKNOWLEDGMENTS

I am grateful to Ellen Tracy and Susan Nesbitt for assistance in the field and laboratory. Dr. C. J. O'Kelly, Massey University, kindly examined our material and confirmed the identification. The work was supported by Natural Sciences and Engineering Research Council grant A 2204.

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# DISCOVERY OF FERNALD'S *BACOPA SIMULANS* (SCROPHULARIACEAE) ON THE POTOMAC RIVER IN VIRGINIA

MARK T. STRONG

The history of *Bacopa simulans* Fernald dates back to 1840, when Rafinesque described *Macuilllamia obovata* Raf. from the Potomac River in Virginia and from Louisiana. Rafinesque (1840) described this species as having prostrate, non-flexuous, hirsute stems; sessile, obovate or elliptic leaves; flowering pedicels shorter than the subtending bract; and globose capsules. In 1921, J. E. Grimes collected three specimens, apparently in very poor condition, along the Chickahominy River at Lanexa, New Kent County, Virginia (*Grimes 4136*, Y). These were labeled as *Echinodorus tenellus* (Mart.) Buchenau. Pennell (1935) identified Grimes' collection as *Macuillamia obovata* Rafinesque. Fernald later formally transferred *M. obovata* to *Bacopa obovata* (Raf.) Fern., never having seen Grimes' collection (Fernald, 1937). Fernald, however, was interested in re-locating Grimes' plant, so he searched the tidal shores along the Chickahominy River in Virginia. In 1941, Fernald finally found what he called the "mysterious *Bacopa*" of Grimes. His material did not agree with Rafinesque's description of *Macuillamia obovata*. Searches were made of herbaria where Rafinesque deposited specimens, both by Pennell in 1935 and by Fernald in 1942. Not a single specimen of *M. obovata* was to be found. According to Fernald, Rafinesque's plant was probably based on a mixture of plants from Louisiana and the shores of the Potomac. He felt that Pennell had recognized this probability, and in his monograph of the Scrophulariaceae in 1935 had tried to sort out characters in the description that would apply either to the plants of Louisiana or to those of the Potomac. Fernald named the Virginia plants *Bacopa simulans*, dismissing Rafinesque's report as presumably *Gratiola virginiana* var. *aestuariorum* Pennell (Fernald, 1942).

Fernald (1942) described *Bacopa simulans* from Graves Landing on the Chickahominy River in Charles City County, Virginia. This area of tidal flats along the Chickahominy has remained the only known historical site for this species. No new specimens of this plant have been collected since Fernald's 1941 collections. All attempts to re-locate the plant have been unsuccessful. *Bacopa*

*simulans* is listed as "historical" on the rare plant element list compiled by the Virginia Natural Heritage Program (VaNHP) in 1986. It is listed as "possibly extinct" (category 2*) by the U.S. Fish and Wildlife Service (1985) and as "extinct" by Ayensu and DeFilipps (1978).

During the summer and fall of 1986, while doing botanical field surveys for the Nature Conservancy, I became familiar with *Bacopa stragula* Fernald in southeastern Virginia. By the end of the season I had developed a good eye for the morphology of this species as well as a good "search image" of the habitat and the species with which it is associated. In early August, 1987, when botanizing the tidal flats along the Potomac River in Stafford County, I came upon four plants that looked very similar to *Bacopa stragula,* but which were much larger and more robust than the plants I had become aquainted with in southeastern Virginia. In the very restricted habitat that the plants occupied, they were scattered over a 2000 ft.$^2$ area. A small specimen was collected and taken to the herbarium of Dr. Ted Bradley at George Mason University in Fairfax, Virginia. Upon examining the specimen, Dr. Bradley and I concluded that it was *Bacopa simulans* as described by Fernald in 1942. The plant was also compared with the isotype specimen at US. It was found to match clearly the morphological characteristics of the isotype.

Fernald (1942) named this species *Bacopa simulans* for its apparent similarity to *B. rotundifolia* (Michaux) Wettstein, a plant of the Mississippi drainage. The latter species was described by Fernald as differing from *B. simulans* in having a "copiously hirsute stem, thin and clearly nerved leaves that are rounded, the larger ones 2–3.5 cm long and 1.5–2.7 cm broad, slender and pubescent pedicels 0.8–2 cm long, and a rather showy campanulate corolla 6–8 mm long, with widespreading limb about as broad." *Bacopa simulans,* on the other hand, was described as having "glabrous stems and pedicels, more opaque leaves only 1–2 cm long and 0.6–1.5 cm broad, thick pedicels at most 11 mm long, and a corolla 4 mm long and 2 mm broad." The specimen I collected from the Potomac River has glabrous stems and pedicels, leaves 0.6–2.0 cm long and 0.6–1.8 cm wide, thick pedicels 0.5–0.8 cm long, and corollas 4 mm long and 2 mm wide, characteristic of *B. simulans.* Specimens are deposited at FARM, GMUF, and in the herbarium of the author.

*Bacopa simulans,* which was once thought to be extinct, is now extant on the Potomac River in Virginia. As of 1988, eleven plants have been found at the site. Because *B. simulans* has been discovered on the Potomac River, protection of its habitat is now of the utmost importance for this rare plant.

## ACKNOWLEDGMENTS

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# *TOXICODENDRON VERNIX* ADDED TO THE FLORA OF NOVA SCOTIA

NICHOLAS M. HILL

During a survey of the distribution of rare coastal plain plants along lakeshores in southwestern Nova Scotia, I discovered two patches of *Toxicodendron vernix* (L.) Kuntze around the inflow to Telfer Lake in Queens County (44°18′N, 65°03′W). Approximately 20 bushes of *T. vernix* grow in the open with scattered trees of *Acer rubrum* L. and various smaller shrubs (*Nemopanthus mucronata* (L.) Trel., *Alnus serrulata* (Ait.) Willd., and *Viburnum cassinoides* L.) on a hummocky point dominated by *Osmunda regalis* L. at the southern end of the lake. Several bushes were fruiting heavily in mid-September and a few dead bushes were observed along the shoreline to the north of the point. The largest bush was 4 m high and stems at ground level were 10 cm in diameter. A second site was found along the south-facing shoreline of the stillwater at the end of Bull Moose Brook. Here, a few bushes of *T. vernix* grow beneath *Acer rubrum* trees in association with *Nemopanthus mucronata, Alnus serrulata* and *Chamaedaphne calyculata* (L.) Moench, with undergrowth of *Glyceria obtusa* (Muhl.) Trin., *Osmunda cinnamamea* L. and *O. regalis.*

The first Canadian report of *Toxicodendron vernix* (under the syn. *Rhus venenata* DC) was from western Ontario (Macoun, 1883). Since then it has been found in eastern Ontario and in southwestern Quebec (Scoggan, 1978). In the United States, *T. vernix* ranges from Texas and Florida to southwest Maine, and extends inland to southeastern Minnesota (Gleason, 1974). Gleason makes no mention of Canadian stations. The present finding of *T. vernix* in Nova Scotia extends its known range by approximately 400 km from the nearest population of the species in Maine to the south and by approximately 550 km from the nearest population to the west in Quebec. It is obviously an addition to the rare vascular plant species of Nova Scotia (Maher et al., 1978). Specimens of *T. vernix* from this newly-discovered site are deposited in ACAD and CAN.

Lakeshores in southwestern Nova Scotia contain many rare coastal plain species which are disjunct from the main part of the species' ranges along the coastal plain of the U.S.A. (Roland and Smith, 1969; Keddy, 1985). Recently, the coastal plain shrub

*Clethra alnifolia* L. was found to be abundant along the boggy shores of two remote lakes in southwestern Nova Scotia (Taschereau, 1969; C. R. K. Allen, unpubl.). *Toxicodendron vernix* is well represented along the coastal plain but also ranges further inland. Two other shrubs, rare in Nova Scotia and restricted to the southwest of the province, were also found along the shores of the secluded Telfer Lake: *Alnus serrulata* has a coastal plain distribution similar to *T. vernix*; *Cephalanthus occidentalis* L. is well represented on the coastal plain but is also found in California and the West Indies.

## ACKNOWLEDGMENTS

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# MAINE'S OFFICIAL LIST OF ENDANGERED AND THREATENED PLANTS

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HARRY R. TYLER, JR., AND BARBARA ST. J. VICKERY

**ABSTRACT**

Maine's Official List of Endangered and Threatened Plants includes 85 Endangered and 74 Threatened taxa. In addition, we have recognized three administrative categories: Special Concern (45 taxa), Special Concern—Possibly Extirpated (90 taxa) and Watch List (37 taxa). Status of a particular plant within Maine is the primary rationale for listing, regardless of frequency of occurrence and abundance outside the state. Lack of knowledge of the biology of most of Maine's rare plants precludes use of biological factors in our criteria. Listing criteria are therefore based on population number and size, with exceptions for plants that are Federally Endangered or Threatened, or with small populations, or confined to a small geographic area, or that are clearly and imminently jeopardized. These exceptions to the criteria allow us to list a plant such as *Carex oronensis,* Orono Sedge, as State Endangered, though it has more than 40 occurrences in Maine, because it is endemic to the Penobscot River drainage. Of Maine's Endangered and Threatened plants, 28 percent are concentrated in the southwestern corner of the state (York and Cumberland Counties) where many plants reach the northeastern limit of their geographical distribution; 38 percent are limited to four areas in northern and northwestern Maine—the St. John River Valley, Crystal Bog, Mt. Katahdin and Twin Peaks. The official list is informational, not regulatory, and will provide a focus for planning and education. The official and administrative lists are to be formally reviewed biennially.

Key Words: Rare, threatened, endangered plants, official list, Maine

Maine's Official List of Endangered and Threatened Plants was established according to Maine law (Title 5:3315 MRSA) on June 23, 1988. This list includes 159 native vascular plant taxa, with 85 Endangered and 74 Threatened (Table 1) representing more than 10% of the approximately 1500 native vascular plant taxa in Maine (Richards et al., 1983). The 90 taxa that are administratively categorized as Special Concern—Possibly Extirpated (Table 1) have no occurrence recorded within the past 20 years, although not all have been sought equally. Two additional administrative categories, Special Concern (45 taxa) and Watch List (37 taxa) (Table 2), are attached to the Official List.

Interest in Maine's rare flora is long-standing and currently strong (Vickery et al., 1989). Since 1973, when the Federal Endangered Species Act (Public Law 93–205) was enacted (Ayensu

Table 1. Maine's Official List of Endangered (E) and Threatened (T) Plants, and Special Concern—Possibly Extirpated (SC-PE) taxa, an administrative category.

In Status—Maine column, E = State Endangered, T = State Threatened and SC-PE = Special Concern—Possibly Extirpated. Letters in parentheses indicate exceptions to the numerical critiera: (a) = small populations; (b) = populations confined to a small geographic area; (c) = populations clearly and imminently jeopardized. In Status—Federal column, LE = Listed Endangered; 2 = listed in the Federal Register (1985), but uncertainties regarding taxonomic status or biological vulnerabilty need to be resolved before the taxon can be listed as Endangered or Threatened at the Federal level; 3B = species status in doubt; 3C = listed in the Federal Register although more abundant or widespread than previously believed, and/or subject to any identifiable threat. Nomenclature follows Kartesz and Kartesz (1980) except where more recent revisions are available.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| **Pteridophytes** | | | |
| Adiantaceae | | | |
| *Cryptogramma stelleri* (Gmel.) Prantl. | Slender Cliff-brake | T | |
| Aspleniaceae | | | |
| *Asplenium platyneuron* (L.) Oakes *ex* D.C. Eat. | Ebony Spleenwort | T | |
| *A. rhizophyllum* L. (*Camptosorus rhyzophyllus*) | Walking Fern | SC-PE | |
| *A. viride* Huds. | Green Spleenwort | E | |
| *Dryopteris filix-mas* (L.) Schott. | Male Fern | E | |
| *Woodsia alpina* (Bolton) S. P. Gray | Northern Woodsia | T | |
| *W. glabella* R. Br. | Smooth Woodsia | T | |
| *W. obtusa* (Spreng.) Torr. | Blunt-lobed Woodsia | T | |
| *Woodwardia areolata* (L.) T. Moore | Netted Chain-fern | SC-PE | |
| Equisetaceae | | | |
| *Equisetum* × *trachyodon* A. Braun (= *E. variegatum* var. *jesupii*) | Scouring Rush | SC-PE | |
| Lycopodiaceae | | | |
| *Lycopodium sabinaefolium* Willd. | Ground-Fir | T | |
| *L. sitchense* Rupr. | Sitka Clubmoss | E | |
| Ophioglossaceae | | | |
| *Botrychium lunaria* (L.) Sw. | Moonwort | E(a) | |
| Selaginellaceae | | | |
| *Selaginella apoda* (L.) Fern. | Creeping Spikemoss | E | |

Table 1. Continued.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| *S. selaginoides* (L.) Link | Northern Spike-moss | SC-PE | |
| **Gymnosperms** | | | |
| Cupressaceae | | | |
| *Chamaecyparis thyoides* (L.) B.S.P. | Atlantic White-Cedar | T(c) | |
| **Angiosperms—Dicotyledons** | | | |
| Apiaceae | | | |
| *Cryptotaenia canadensis* (L.) DC. | Wild Chervil | SC-PE | |
| *Osmorhiza chilensis* Hook. & Arn. | Western Sweet Cicely | T | |
| Aquifoliaceae | | | |
| *Ilex glabra* (L.) Gray | Inkberry | E | |
| Araliaceae | | | |
| *Panax quinquefolius* L. | American Gin-seng | T(c) | 3C |
| Aristolochiaceae | | | |
| *Asarum canadense* L. | Wild Ginger | T(c) | |
| Asclepiadaceae | | | |
| *Asclepias tuberosa* L. | Butterfly-weed | E | |
| Asteraceae | | | |
| *Aster divaricatus* L. | White Wood Aster | T | |
| *A. dumosus* L. | Bush Aster | E | |
| *A. foliaceus* Lindl. | Leafy-bracted Aster | T | |
| *A. patens* Ait. | Late Purple Aster | SC-PE | |
| *A. paternus* Cronq. | White-topped Aster | T | |
| *A. schreberi* Nees | Schreber's Aster | SC-PE | |
| *A. subulatus* Michx. | Small Salt-marsh Aster | E | |
| *Bidens eatonii* Fern. | Eaton's Bur-marigold | T | |
| *B. hyperborea* Greene | Estuary Bur-marigold | T | |
| *Erigeron acris* L. var. *kamschatikus* (DC.) Herder (= *E. angulosus* var. *k.*) | Fleabane | SC-PE | |
| *Eupatorium dubium* Willd. *ex* Poir. | Eastern Joe-Pye-Weed | E | |
| *E. fistulosum* Barratt | Trumpet-Weed | SC-PE | |

Table 1. Continued.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| *E. rotundifolium* L. var. *ovatum* (Bigelow) Torr. (= *E. pubescens*) | Hairy Boneset | SC-PE | |
| *Gnaphalium purpureum* L. | Purple Cudweed | SC-PE | |
| *G. supinum* L. | Alpine Cudweed | E | |
| *Hieracium gronovii* L. | Gronovius' Hawkweed | SC-PE | |
| *H. robinsonii* (Zahn) Fern. | Robinson's Hawkweed | SC-PE | |
| *H. venosum* L. var. *nudicaule* (Michx.) Farw. | Poor Robin's Plantain | SC-PE | |
| *Iva frutescens* L. var. *oraria* (Bartlett) R.C. Jackson | Marsh-elder | T | |
| *Liatris scariosa* (L.) Willd. var. *novae-angliae* (Lunnell) (= *L. borealis* Nutt.) | Northern Blazing Star | T | |
| *Mikania scandens* (L.) Willd. | Climbing Hempweed | SC-PE | |
| *Prenanthes boottii* (DC.) Gray | Boott's Rattlesnake-root | T | 2 |
| *P.* × *mainensis* Gray | Hybrid Rattlesnake Root | SC-PE | |
| *P. nana* (Bigelow) Torr. (= *P. trifoliolata* var. *nana*) | Dwarf Rattlesnake-root | E | |
| *Solidago calcicola* Fern. | Rock Goldenrod | SC-PE | |
| *S. ulmifolia* Muhl. | Elm-leaved Goldenrod | SC-PE | |
| *Tanacetum bipinnatum* (L.) Schultz-Bip. ssp. *huronense* (Nutt.) Breitung (= *T. h.* var. *johannense*) | Saint John Tansy | T(b) | |
| Balsaminaceae | | | |
| *Impatiens pallida* Nutt. | Yellow Jewelweed | T | |
| Betulaceae | | | |
| *Betula glandulosa* Michx. | Dwarf Birch | E | |
| *B. minor* (Tuckerman) Fern. | Dwarf White Birch | E | |
| Boraginaceae | | | |
| *Hackelia deflexa* (Wahlenb.) Opiz var. *americana* (Gray) Fern. & I. M. Johnston (= *H. americana*) | American Stickseed | E | |
| Brassicaceae | | | |
| *Arabis divaricarpa* A. Nels. | Purple Rockcress | SC-PE | |

Table 1. Continued.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| *A. laevigata* (Muhl.) Poir. | Smooth Rock-cress | E(a) | |
| *A. missouriensis* Greene | Missouri Rock-cress | T | |
| *Barbarea orthoceras* Ledeb. | Winter-cress | SC-PE | |
| *Cardamine bellidifolia* L. | Bitter-cress | E | |
| *C. longii* Fern. | Long's Bitter-cress | T(b) | 2 |
| *Dentaria laciniata* Muhl. ex Willd. | Cut-leaved Toothwort | E | |
| *D. maxima* Nutt. | Great Toothwort | SC-PE | |
| *Descurainia richardsonii* (Sweet) O. E. Schulz | Richardson's Tansy-mustard | SC-PE | |
| *Draba arabisans* Michx. | Rock Whitlow-Grass | T | |
| *D. lanceolata* | Lance-leaved Draba | E | |
| Callitrichaceae | | | |
| *Callitriche anceps* Fern. | Water-Starwort | E | |
| Campanulaceae | | | |
| *Lobelia siphilitica* L. | Blue Cardinal Flower | SC-PE | |
| Caprifoliaceae | | | |
| *Lonicera dioica* L. | Mountain Honeysuckle | E(a) | |
| *L. sempervirens* L. | Trumpet Honey-suckle | SC-PE | |
| *Triosteum aurantiacum* Bickn. | Wild-Coffee | T | |
| Caryophyllaceae | | | |
| *Minuartia rubella* (Wahlenb.) Hiern (*Arenaria r.*) | Arctic Sandwort | E | |
| *Silene acaulis* (L.) Jacq. var. *acaulis* (= *S. a.* var. *exscapa*) | Moss Campion | SC-PE | |
| Chenopodiaceae | | | |
| *Chenopodium berlanderi* Moq. var. *boscianum* (Moq.) H. A. Wahl (= *C. boscianum*) | Bosc's Goosefoot | E | |
| *C. rubrum* L. | Coast-Blite | T | |
| *Salicornia virginica* L. (= *S. bigelovii*) | Dwarf Glasswort | E | |
| *Suaeda americana* (Pers.) Fern. | American Sea-blite | SC-PE | |
| *S. richii* Fern. | Rich's Sea-blite | E | |

Table 1. Continued.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| Cistaceae | | | |
| *Lechea tenuifolia* Michx. | Slender Pinweed | SC-PE | |
| Clethraceae | | | |
| *Clethra alnifolia* L. | Sweet Pepper-bush | T(c) | |
| Clusiaceae | | | |
| *Hypericum pyramidatum* Ait. | Great St. Johns-wort | SC-PE | |
| Convolvulaceae | | | |
| *Calystegia spithamaea* (L.) Pursh | Upright Bind-weed | T | |
| Cornaceae | | | |
| *Cornus florida* L. | Flowering Dog-wood | E(a) | |
| Droseraceae | | | |
| *Drosera anglica* Huds. | English Sundew | E | |
| *D. linearis* Goldie | Linear-leaf Sundew | E | |
| Elaeagnaceae | | | |
| *Shepherdia canadensis* (L.) Nutt. | Canada Buffalo-berry | E | |
| Ericaceae | | | |
| *Arctostaphylos alpina* (L.) Spreng. | Alpine Bearberry | T | |
| *Cassiope hypnoides* (L.) D. Don | Moss Plant | E | |
| *Loiseleuria procumbens* (L.) Desv. | Alpine Azalea | E | |
| *Phyllodoce caerulea* (L.) Bab. | Mountain Heath | E | |
| *Rhododendron lapponicum* (L.) Wahlenb. | Lapland Rose-bay | E | |
| *R. maximum* L. | Great Rhodo-dendron | T(c) | |
| *R. viscosum* (L.) Torr. | Clammy Azalea | T | |
| *Vaccinium boreale* Hall & Aalders | Alpine Blueberry | SC-PE | |
| Euphorbiaceae | | | |
| *Acalypha virginica* L. | Three-seeded Mercury | SC-PE | |
| Fabaceae | | | |
| *Astragalus eucosmus* B.L. Robins | Elegant Milk-vetch | SC-PE | |
| *A. robbinsii* (Oakes) Gray var. *minor* (Hook.) Barneby | Robbin's Milk-vetch | SC-PE | |
| *Baptisia tinctoria* (L.) R. Br. var. *crebra* Fern. | Wild Indigo | E | |
| *Lespedeza* × *nuttallii* Darl. (*L.* × *n.*) | Nuttall's Bush Clover | SC-PE | |

Table 1. Continued.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| *L. hirta* (L.) Hornem. | Hairy Bush-clover | SC-PE | |
| *Lupinus perennis* L. | Wild Lupine | SC-PE | |
| *Oxytropis campestris* (L.) DC. var. *johannensis* Fern. | St. John Oxytrope | T(b) | 2 |
| Fagaceae | | | |
| *Quercus coccinea* Muenchh. | Scarlet Oak | SC-PE | |
| *Q. montana* Willd. (= *Q. prinus*) | Chestnut Oak | E | |
| Gentianaceae | | | |
| *Bartonia paniculata* (Michx.) Muhl. | Screw-stem | E | |
| *Gentiana rubricaulis* Schwein. | Red-stemmed Gentian | SC-PE | |
| *Gentianella amarella* (L.) Borner (*Gentiana a.*) | Northern Gentian | E | |
| *G. quinquefolia* (L.) Small | Stiff Gentian | SC-PE | |
| Juglandaceae | | | |
| *Carya cordiformis* (Wang) K. Koch | Bitternut Hickory | E | |
| Lamiaceae | | | |
| *Scutellaria leonardii* Epling | Leonard's Skullcap | SC-PE | |
| *S. parvula* Michx. | Small Skullcap | SC-PE | |
| *Stachys tenuifolia* Willd. var. *hispida* (Pursh) Fern. (= *S. t.* var. *platyphylla*) | Thin-leaved Hedge-nettle | SC-PE | |
| Lentibulariaceae | | | |
| *Utricularia resupinata* B. D. Greene | Small Purple Bladderwort | T | |
| Onagraceae | | | |
| *Epilobium anagallidifolium* Lam. (= *E. alpinum*) | Alpine Willow-herb | T | |
| *E. ciliatum* Raf. | Hairy Willow-herb | T | |
| *E. hornemannii* Reichenb. | Hornemann's Willow-herb | T | |
| Papaveraceae | | | |
| *Adlumia fungosa* (Ait.) Greene *ex* B.S.P. | Allegheny Vine | E | |
| *Dicentra canadensis* (Goldie) Walp. | Squirrel-corn | T | |
| Platanaceae | | | |
| *Platanus occidentalis* L. | Sycamore | SC-PE | |

Table 1. Continued.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| Polemoniaceae | | | |
| *Polemonium vanbruntiae* Britt. | Jacob's Ladder | E | |
| Polygalaceae | | | |
| *Polygala cruciata* L. (*P. c.* var. *aquilonia*) | Marsh Milkwort | SC-PE | |
| *P. senega* L. | Seneca Snake-root | T | |
| Polygonaceae | | | |
| *Polygonum douglasii* Greene | Douglas' Knot-weed | T | |
| *P. viviparum* L. | Alpine Bistort | E | |
| *Rumex occidentalis* S. Wats. var. *fenestratus* (Greene) Lepage (=*Rumex fenestratus*) | Dock | SC-PE | |
| Primulaceae | | | |
| *Hottonia inflata* Ell. | Feather-foil | SC-PE | |
| Ranunculaceae | | | |
| *Anemone multifida* Poir. | Cut-leaved Anemone | T(a,b) | |
| *Hepatica nobilis* P. Mill. var. *acuta* (Pursh) Steyermark (*H. acutiloba*) | Sharp-lobed Hepatica | SC-PE | |
| *Ranunculus ambigens* S. Wats. | Water-plantain Spearwort | SC-PE | |
| *R. fascicularis* Muhl. *ex* Bigelow | Early Crowfoot | T | |
| *R. gmelini* DC. | Small Yellow Water-Crowfoot | T | |
| *R. lapponicus* L. | Lapland Buttercup | T | |
| *Thalictrum thalictroides* (L.) Eames & Boivin (*Anemonella t.*) | Rue-Anemone | SC-PE | |
| *T. venulosum* Trel. var. *confine* (Fern.) B. Boivin (= *T. turneri*; formerly *T. confine*) | Boundary Meadow-Rue | SC-PE | |
| Rhamnaceae | | | |
| *Ceanothus americanus* L. | New Jersey Tea | T(c) | |
| Rosaceae | | | |
| *Amelanchier humilis* Wieg. | Low Shadbush | E | |
| *Sanguisorba canadensis* L. | Canada Burnet | SC-PE | |
| *Spiraea septentrionalis* (Fern.) Love & Love (=*S. latifolia* var. *s.*) | Northern Meadowsweet | E | |

Table 1. Continued.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| *Waldsteinia fragarioides* (Michx.) Tratt. | Barren-Strawberry | T | |
| Rubiaceae | | | |
| *Galium obtusum* Bigelow | Blunt-leaved Bedstraw | SC-PE | |
| *Hedyotis purpurea* (L.) Torr. & Gray var. *calycosa* (Gray) Fosberg (*Houstonia lanceolata*) | Lance-leaved Bluet | SC-PE | |
| Salicaceae | | | |
| *Salix arctophila* Cockerell *ex* Heller | Arctic Willow | E | |
| *S. argyrocarpa* Anderss. | Silverleaf Willow | SC-PE | |
| *S. candida* Flugge *ex* Willd. | Hoary Willow | T | |
| *S. cordata* Michx. | Heartleaf Willow | SC-PE | |
| *S. exigua* Nutt. (= *S. interior* var. *exterior*) | Sandbar Willow | T | 3B |
| *S. herbacea* L. | Dwarf Willow | E | |
| *S. pedicellaris* Pursh | Bog Willow | SC-PE | |
| *S. planifolia* Pursh | Flatleaf Willow | E | |
| *S. uva-ursi* Pursh | Bearberry Willow | T | |
| Saxifragaceae | | | |
| *Saxifraga foliolosa* R. Br. var. *foliolosa* (= *S. stellaris* var. *comosa*) | Star Saxifrage | E | |
| *S. paniculata* P. Mill. (= *S. aizoon* var. *neogaea*) | Livelong Saxifrage | T | |
| *S. pensylvanica* L. | Swamp Saxifrage | T(b,c) | |
| Scrophulariaceae | | | |
| *Agalinis neoscotica* (Greene) Fern. | Nova Scotia Agalinis | E | |
| *Euphrasia disjuncta* Fern. & Wieg. | Disjunct Eyebright | SC-PE | |
| *E. oakesii* Wettst. | Oakes' Eyebright | E | |
| *Pedicularis furbishiae* S. Wats. | Furbish's Lousewort | E | LE |
| *Scrophularia marilandica* L. | Carpenter's Square | SC-PE | |
| *Veronica wormskjoldii* Roemer & Schultes ssp. *wormskjoldii* (= *V. alpina* var. *unalaschensis*) | Alpine Speedwell | E | |
| Ulmaceae | | | |
| *Ulmus rubra* Muhl. | Slippery Elm | SC-PE | |

Table 1. Continued.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| Urticaceae | | | |
| *Parietaria pensylvanica* Muhl. *ex* Willd. | Pennsylvania Pellitory | SC-PE | |
| Verbenaceae | | | |
| *Phryma leptostachya* L. (formerly in Phrymaceae) | Lopseed | SC-PE | |
| *Verbena urticifolia* L. | White Vervain | SC-PE | |
| Violaceae | | | |
| *Viola adunca* Sm. var. *minor* | Violet | SC-PE | |
| *V. brittoniana* Pollard | Coast Violet | SC-PE | |
| *V. palustris* L. | Alpine Marsh Violet | E | |
| *V. triloba* Schwein. | Three-lobed Violet | SC-PE | |
| Vitaceae | | | |
| *Vitis aestivalis* Michx. (= *V. a.* var. *argentifolia*) | Summer Grape | T | |
| **Angiosperms—Monocotyledons** | | | |
| Alismaceae (Alismataceae) | | | |
| *Sagittaria rigida* Pursh | Stiff Arrowhead | E | |
| Cyperaceae | | | |
| *Carex adusta* Boott | Sedge | SC-PE | |
| *C. alopecoidea* Tuckerman | Fox-tail Sedge | E | |
| *C. atherodes* Spreng. | Awned Sedge | SC-PE | |
| *C. bushii* Mackenzie | Bush's Sedge | SC-PE | |
| *C. crawei* Dewey | Crawe's Sedge | SC-PE | |
| *C. eburnea* Boott | Ebony Sedge | T | |
| *C. echinata* Murr. | Little Prickly Sedge | T | |
| *C. gynocrates* Wormskj. *ex* Drej. | Sedge | T | |
| *C. livida* (Wahlenb.) Willd. var. *grayana* (Dewey) Fern. | Livid Sedge | T | |
| *C.* ×*mainensis* Porter | Sedge | SC-PE | |
| *C. media* R. Br. | Intermediate Sedge | E | |
| *C. oronensis* Fern. | Orono Sedge | E(a,b) | 2 |
| *C. polymorpha* Muhl. | Variable Sedge | T | 2 |
| *C. prairea* Dewey | Prairie Sedge | T | |
| *C. praticola* Rydb. | Sedge | SC-PE | |
| *C. rariflora* (Wahlenb.) Sm. | Loose-flowered Sedge | SC-PE | |
| *C. salina* Wahlenb. var. *kattegatensis* (Fries) Almquist | Salt-marsh Sedge | E | |

Table 1. Continued.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| *C. saxatilis* L. | Russett Sedge | E | |
| *C. scirpoidea* Michx. | Bulrush Sedge | T | |
| *C. sparganioides* Willd. | Bur-Reed Sedge | E | |
| *C. sterilis* Willd. | Atlantic Sedge | T | |
| *C.* ×*trichina* Fern. | Sedge | SC-PE | |
| *C. typhina* Michx. | Cat-tail Sedge | SC-PE | |
| *C. vaginata* Tausch | Sheathed Sedge | T | |
| *Cyperus houghtonii* Torr. | Houghton's Umbrella Sedge | SC-PE | |
| *Eleocharis pauciflora* (Lightf.) Link (= *E. p.* var. *fernaldii*) | Spike-rush | E | |
| *E. rostellata* (Torr.) Torr. | Beaked Spike-rush | E | |
| *E. tuberculosa* (Michx.) Roemer & Schultes | Long-tubercled Spike-rush | E | |
| *Hemicarpha micrantha* (Vahl) Britt. | Dwarf Bulrush | T | |
| *Rhynchospora capillacea* Torr. | Beak-Rush | E | |
| *R. macrostachya* Gray | Horned-rush | SC-PE | |
| *Scirpus longii* Fern. | Long's Bulrush | SC-PE | 2 |
| *S. pendulus* Muhl. | Pendulous Bulrush | SC-PE | |
| Juncaceae | | | |
| *Juncus alpinus* Vill. | Alpine Rush | T | |
| *J. oronensis* Fern. | Orono Rush | SC-PE | |
| *J. subtilis* E. Mey. | Rush | SC-PE | |
| *Luzula confusa* Lindeberg | Northern Woodrush | E | |
| *L. spicata* (L.) DC. | Spiked Woodrush | E | |
| Iridaceae | | | |
| *Iris prismatica* Pursh | Slender Blue-flag | T | |
| Lemnaceae | | | |
| *Wolffia columbiana* Karst. | Columbia Water-meal | T | |
| Liliaceae | | | |
| *Aletris farinosa* L. | Unicorn-root | SC-PE | |
| *Hypoxis hirsuta* (L.) Coville (formerly in Amaryllidaceae) | Stargrass | SC-PE | |
| *Streptopus* ×*oreopolus* Fern. | Twisted Stalks hybrid | SC-PE | |
| *Trillium grandiflorum* (Michx.) Salisb. | Large-flowered Trillium | SC-PE | |

Table 1. Continued.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| Najadaceae | | | |
| *Najas guadalupensis* (Spreng.) Magnus | Guadalupe Naiad | SC-PE | |
| Orchidaceae | | | |
| *Amerorchis rotundifolia* (Banks *ex* Pursh) Hulten (*Orchis r.*) | Small Round-leaved Orchis | T | |
| *Corallorhiza odontorhiza* (Willd.) Nutt. | Autumn Coral Root | E(a) | |
| *Cypripedium arietinum* R. Br. | Ram's Head Lady's Slipper | T | 3C |
| *Galearis spectabilis* (L.) Raf. (= *Orchis s.*) | Showy Orchis | T | |
| *Goodyera oblongifolia* Raf. | Giant Rattle-snake-plantain | E(c) | |
| *Isotria medeoloides* (Pursh) Raf. | Small Whorled Pogonia | E | LE |
| *I. verticillata* (Muhl. *ex* Willd.) Raf. | Large Whorled Pogonia | E | |
| *Malaxis brachypoda* (Gray) Fern. | White Adder's-mouth | E | |
| *Platanthera leucophaea* (Nutt.) Lindl. | Prairie White-fringed Orchid | E | 2 |
| *Spiranthes lucida* (A. A. Eat.) Ames | Shining Ladies'-tresses | T(a) | |
| *Triphora trianthophora* (Sw.) Rydb. | Nodding Pogonia | T(b) | |
| Poaceae | | | |
| *Bromus kalmii* Gray | Kalm's Brome Grass | E | |
| *B. pubescens* Muhl. *ex* Willd. | Brome Grass | E | |
| *Calamagrostis cinnoides* (Muhl.) Bart. | Reed-Bentgrass | SC-PE | |
| *C. pickeringii* Gray | Reed-Bentgrass | E | |
| *C. stricta* (Timm) Koel. ssp. *inexpansa* (Gray) C. W. Greene (= *C. fernaldii*) (= *C. inexpansa* var. *novae-angliae*) | Reed-Bentgrass | T | |
| *C. stricta* (Timm) Koel. ssp. *stricta* (= *C. neglecta*) | Reed-Bentgrass | SC-PE | |
| *Deschampsia atropurpurea* (Wahlenb.) Scheele | Hairgrass | E | |
| *Eragrostis capillaris* (L.) Nees | Lace-Grass | E | |
| *Festuca rubra* L. var. *prolifera* Piper | Proliferous Red Fescue | E | |

Table 1. Continued.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| *Hierochloe alpina* (Willd.) Roemer & Schultes | Alpine Holygrass | T | |
| *Muhlenbergia sobolifera* (Muhl.) Trin. | Cliff Muhly Grass | E | |
| *Phleum alpinum* L. | Mountain Timothy | T | |
| *Poa fernaldiana* Nannf. | Wavy Bluegrass | E | |
| *Spartina* ×*caespitosa* (A. A. Eat.) Fern. | Cord-Grass | SC-PE | |
| *Sphenopholis obtusata* (Michx.) Scribn. | Prairie Wedgegrass | SC-PE | |
| *Sporobolus asper* (Michx.) Kunth | Drop-Seed Grass | E | |
| *Trisetum melicoides* (Michx.) Scribn. | Purple False Oats | E | |
| *T. triflorum* (Bigelow) Love & Love (= *T. spicatum* var. *pilosiglume*) | Narrow False Oats | T | |
| Pontederiaceae | | | |
| *Heteranthera dubia* (Jacq.) MacM. | Water Stargrass | E | |
| Potamogetonaceae | | | |
| *Potamogeton confervoides* Reichenb. | Pondweed | T | |
| *P. friesii* Rupr. | Fries' Pondweed | E | |
| *P. pulcher* Tuckerman | Pondweed | T | |
| *P. vaseyi* J. W. Robbins | Vasey's Pondweed | E | |
| Scheuchzeriaceae | | | |
| *Triglochin gaspense* Lieth & D. Love | Gaspe Arrowgrass | SC-PE | |
| Xyridaceae | | | |
| *Xyris smalliana* Nash | Yellow-eyed Grass | E | |

and DeFilipps, 1978), there has been an increasing effort in Maine to inventory and conserve plants thought to be rare. Many individuals and two organizations in particular—first the Critical Areas Program of the Maine State Planning Office and later the Natural Heritage Program of the Maine Chapter of The Nature Conservancy—have supported herbarium and field studies (Eastman, 1978a, 1978b; Gawler, 1978, 1984; Tyler and Gawler, 1980;

Critical Areas Program, 1985b). Information on the status of Maine's rare plants is available in *Rare Vascular Plants of Maine* (Critical Areas Program, 1985a) and its 1986 Addendum (Vickery et al., 1986) and from the Maine Natural Heritage Program of the Nature Conservancy.

## ESTABLISHING THE OFFICIAL LIST

In 1986 the Maine State Legislature passed an Act to Establish an Official List of Endangered and Threatened Plants (Title 5: 3315 MRSA) and directed the Critical Areas Program to establish the state's official list. An Endangered Plant Technical Advisory Committee, composed of botanists, educators, conservationists, a lawyer, and representatives from major commercial landholders prepared a draft of an official list (*see* Acknowledgments for names of committee members).

To obtain possible models for Maine's criteria for listing Endangered, Threatened and Special Concern—Possibly Extirpated plants, we sent a questionnaire to 48 states inquiring about their criteria. Thirty-three states responded; all had a list, though they used diverse approaches in drawing up these lists. The standardization of criteria called for by Ayensu (1981) has not been accomplished. Many states' lists follow closely the element ranking system of the Natural Heritage Program, which reflects the number of known and established occurrences for a species in a state. Other states derive their lists by incorporating quantified data with allowances made for unusual species biology. Subspecies and varieties are included by many states (but not on Maine's official list unless the subspecific taxon represents the species in Maine, or the taxon is listed in the Federal Register, or there are ten or fewer recent occurrences in Maine), and hybrids are excluded unless fertile.

Most states follow the definition of taxon categories in the Federal Register (1985) and include in their list Federally listed plant species. Federal listing covers plants that occur in the U.S.A. and are Endangered or Threatened globally. Two Federally-listed Endangered species, *Pedicularis furbishiae* (Furbish's Lousewort) and *Isotria medeoloides* (Small Whorled Pogonia), grow in Maine and are on Maine's list as State Endangered.

Almost all states that responded to our questionnaire list plants

that are Endangered or Threatened within the state even if they are not rare elsewhere. Many states (e.g., California, Idaho, Michigan, Tennessee and Wisconsin) also consider status outside the state. Others (e.g., North Carolina, Washington and Wisconsin) give priority to disjunctions according to distance from the main population. Maine's list is based on Endangered and Threatened status within the state, regardless of status outside state boundaries.

We believe that criteria used should closely correspond to legal definitions of Endangered and Threatened. In addition, they should be clear enough for the lay public to comprehend and apply. Our list is intended to reflect biological endangerment, not simply scarcity. However, it is often difficult to assess "threat" in natural systems, especially in view of the paucity of data for many rare plant species. Often the only quantifiable indicators of need for protection are number and size of populations. Hence our primary criterion is numerical—the number of documented, recent occurrences in the state and the population size. "Recent" is within 20 years, a time frame we consider workable because 50 years, which was originally proposed, would have made the Endangered list more than twice as long and not as up-to-date. Native plants formerly known from Maine but not seen within 20 years were placed in the Special Concern—Possibly Extirpated category. "Occurrence" refers to natural, indigenous existence, either as a population (a group of individuals of the same taxon growing in one place) or in a town (if there is more than one documentation from the town but best available data do not indicate more than one population). Our numerical criteria are stringent enough to avoid a list so large as to undermine its credibility or the willingness of developers, planners and landowners to cooperate in voluntary conservation.

Maine's criteria are most similar to those of Rhode Island and Wisconsin in that a single known, recent occurrence automatically qualifies a taxon as Endangered. In addition, Maine's Endangered status includes any Federally Endangered plants. Exceptions to the strictly numerical criteria allow us to accommodate certain biological realities for plants that would not otherwise be included. Such exceptions are made for taxa with more than one occurrence but with small population sizes, for populations confined to a small geographic area, or for plants clearly and imminently in jeopardy due to disease, human activity, or other causes.

*Bartonia paniculata,* Screwstem, is State Endangered because of only a single known, recent occurrence in Maine on a large coastal island. *Cassiope hypnoides, Loiseleuria procumbens,* and *Phyllodoce caerulea,* which all occur only on Mt. Katahdin in Maine, are also State Endangered. *Botrychium lunaria* is Endangered because one of its two populations in Maine totals a few individuals. *Corallorhiza odontorhiza* and *Lonicera dioica* are also listed as Endangered because in each case the two known populations in Maine are very small, with one population consisting of fewer than 10 individuals.

These criteria also allow for unusual cases such as *Carex oronensis* (Orono Sedge), which is Federally listed as category "2," a designation for taxa that may be appropriate to list but that require further data on biological vulnerability, taxonomy and/or threats (Federal Register, 1985). *Carex oronensis* is endemic to a single watershed in Maine (Eastman, 1980) and is the only vascular plant taxon that occurs solely in Maine. An extensive survey in 1987–1988 resulted in the location of 41 occurrences of *C. oronensis,* all within the Penobscot River drainage (Dibble, unpubl. data); the taxon therefore is possibly at risk. Taxonomic status is not yet resolved for *C. oronensis.*

Threatened status parallels Endangered, except that the numerical criterion is two to four populations. Currently there are no Federally Threatened taxa in Maine. The above exceptions to Endangered status regarding population size, etc. also apply to the Threatened category. *Impatiens pallida* meets the numerical criterion, with four populations in Maine, so it receives Threatened status. *Panax quinquefolius* is Threatened despite 10 recent occurrences because it is commercially exploited. *Cypripedium reginae,* with at least 40 recent occurrences, is Threatened because of overpicking and digging from natural populations.

Maine's three administrative categories, Special Concern—Possibly Extirpated (Table 1), Special Concern and Watch List (Table 2), contain taxa that are potential additions to Endangered and Threatened categories in the future. These lists provide valuable information about rare plants in the State.

The Special Concern—Possibly Extirpated category is for plants not documented in 20 years. Many of these plants have not yet been sought diligently. *Trillium grandiflorum, Hepatica nobilis* var. *acuta. Lupinus perennis* and *Carex rariflora* have been sought through the years but not re-located. These taxa are not necessarily

Table 2. Maine's administrative lists of plants that are Special Concern (SC) and Watch List (WL).

In Status—Federal column, 2 = listed in the Federal Register (1985) but uncertainties regarding taxonomic status or biological vulnerability need to be resolved before the taxon can be listed as Federally Endangered; 3B = species status in doubt; 3C = listed in the Federal Register although more abundant or widespread than previously believed, and/or subject to any identifiable threat. Nomenclature follows Kartesz and Kartesz (1980) except where more recent revisions are available.

| Scientific name | Common name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| **Pteridophytes** | | | |
| Adiantaceae | | | |
| *Adiantum pedatum* L. var. *aleuticum* Rupr. | Aleutian Maidenhair Fern | WL | |
| Aspleniaceae | | | |
| *Dryopteris fragrans* (L.) Schott. | Fragrant Cliff-fern | SC | |
| *D. goldiana* (Hook.) Gray | Goldie's Fern | SC | |
| Equisetaceae | | | |
| *Equisetum variegatum* Schleich. *ex* Weber & C. Mohr | Variegated Scouring Rush | SC | |
| Lycopodiaceae | | | |
| *Lycopodium selago* L. | Alpine Clubmoss | SC | |
| **Angiosperms—Dicotyledons** | | | |
| Apiaceae | | | |
| *Lilaeopsis chinensis* (L.) Kuntze | Lilaeopsis | SC | |
| Aquifoliaceae | | | |
| *Ilex laevigata* (Pursh) Gray | Smooth Winterberry Holly | WL | |
| Araceae | | | |
| *Peltandra virginica* Raf. | Arrow-Arum | SC | |
| Asteraceae | | | |
| *Arnica mollis* Hook. | Arnica | SC | |
| *Aster borealis* (Torr. & Gray) Prov. (= *A. junciformis*) | Rush Aster | SC | |
| *Erigeron hyssopifolius* Michx. | Hyssop-leaved Fleabane | WL | |
| *Prenanthes racemosa* Michx. | Racemed Rattlesnake-root | SC | |
| *Solidago canadensis* L. var. *salebrosa* (Piper) M. E. Jones | Goldenrod | WL | |
| *S. canadensis* L. var. *scabra* (Muhl.) Torr. & Gray | Goldenrod | WL | |
| *S. canadensis* L. var *subserrata* (DC.) Cronq. | Goldenrod | WL | |

Table 2. Continued.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| *S. cutleri* Fern. | Cutler's Goldenrod | SC | |
| Betulaceae | | | |
| *Betula* ×*caerulea* Blanch. (= *B. c. grandis*) | Blue Birch | SC | |
| *B. pumila* L. | Bog Birch | SC | |
| Brassicaceae | | | |
| *Subularia aquatica* L. | Awlwort | SC | |
| Caprifoliaceae | | | |
| *Lonicera oblongifolia* (Goldie) Hook. | Swamp Honeysuckle | SC | |
| *Viburnum edule* (Michx.) Raf. | Squashberry, Mooseberry | WL | |
| Caryophyllaceae | | | |
| *Minuartia glabra* (Michx.) Mattf. (= *Arenaria glabra*) | Smooth Sandwort | WL | |
| *M. groenlandica* (Retz.) Ostenf. (= *Arenaria groenlandica*) | Mountain Sandwort | WL | |
| *Paronychia argyrocoma* (Michx.) Nutt. (= *P. a.* var. *albimontana*) | White Mountain Silverling | SC | 3B |
| *Sagina nodosa* L. Fenzl ssp. *borealis* Crow | Pearlwort | WL | |
| *S. nodosa* L. Fenzl ssp. *nodosa* | Pearlwort | WL | |
| Crassulaceae | | | |
| *Crassula aquatica* (L.) Schoenl. (= *Tillaea a.*) | Pygmyweed | SC | |
| Diapensiaceae | | | |
| *Diapensia lapponica* L. | Diapensia | SC | |
| Ericaceae | | | |
| *Chimaphila maculata* (L.) Pursh | Spotted Wintergreen | SC | |
| *Kalmia latifolia* L. | Mountain-Laurel | WL | |
| *Pyrola asarifolia* Michx. | Purple Pyrola | WL | |
| Fabaceae | | | |
| *Astragalus alpinus* L. var. *brunetianus* Fern. | Alpine Milkvetch | SC | |
| *Hedysarum alpinum* L. var. *alpinum* (= *H. a.* var. *americanum*) | Alpine Sweetbroom | SC | |
| Fagaceae | | | |
| *Castanea dentata* (Marsh.) Borkh. | American Chestnut | SC | |
| Gentianaceae | | | |
| *Gentianopsis crinita* (Froel.) Ma (= *Gentiana c.*) | Fringed Gentian | WL | |

Table 2. Continued.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| Lauraceae | | | |
| *Lindera benzoin* (L.) Blume | Spicebush | SC | |
| *Sassafras albidum* (Nutt.) Nees | Sassafras | SC | |
| Nymphaeaceae | | | |
| *Nymphaea tetragona* Georgi | Pygmy Water Lily | SC | |
| Plantaginaceae | | | |
| *Littorella americana* Fern. | Littorella | SC | |
| Podostemaceae | | | |
| *Podostemon ceratophyllum* Michx. (= *Podostemum c.*) | Threadfoot | WL | |
| Portulacaceae | | | |
| *Montia fontana* L. (=*M. lamprosperma*) | Blinks | SC | |
| Potamogetonaceae | | | |
| *Potamogeton filiformis* Pers. | Pondweed | SC | |
| Primulaceae | | | |
| *Primula farinosa* L. (= *P. laurentiana*) | Bird's-eye Primrose | WL | |
| *P. mistassinica* Michx. | Mistassini Primrose | WL | 3C |
| *Samolus valerandi* L. ssp. *parviflorus* (Raf.) Hulten (= *S. parviflorus*) | Water-pimpernel | WL | |
| Ranunculaceae | | | |
| *Clematis occidentalis* (Hornem.) DC. (= *C. verticillaris*) | Purple Clematis | SC | |
| Rosaceae | | | |
| *Rubus chamaemorus* L. | Baked-apple Berry | WL | |
| Rubiaceae | | | |
| *Hedyotis longifolia* (Gaertn.) Hook. (= *Houstonia l.*) | Long-leaved Bluet | WL | |
| Santalaceae | | | |
| *Geocaulon lividum* (Richards) Fern. | Northern Comandra | SC | |
| Saxifragaceae | | | |
| *Parnassia glauca* Raf. | Grass-of-Parnassus | WL | |
| Scrophulariaceae | | | |
| *Agalinis martima* (Raf.) Raf. | Seaside Agalinis | WL | |
| *Castilleja septentrionalis* Lindl. | Northern Painted-cup | WL | |

Table 2. Continued.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| *Limosella australis* R. Br. (= *L. subulata*) | Mudwort | WL | |
| *Lindernia dubia* (L.) Pennell var. *anagallidea* (Michx.) Cooperrider (= *L. anagallidea*) | False Pimpernel | WL | |
| *Mimulus ringens* L. var. *copophilus* Fern. | Estuarine Monkey Flower | WL | 2 |
| Valerianaceae | | | |
| *Valeriana sitchense* Bong. ssp. *uliginosa* (Torr. & Gray) F. G. Mey. (= *V. uliginosa*) | Northern Valerian | SC | 3C |
| Violaceae | | | |
| *Viola novae-angliae* House | New England Violet | SC | 2 |
| **Angiosperms—Monocotyledons** | | | |
| Alismaceae (= Alismataceae) | | | |
| *Sagittaria calycina* Engelm. var. *spongiosa* Englem. (= *S. montevidensis* var. *s.*) | Arrowhead | WL | |
| Cyperaceae | | | |
| *Carex flava* L. var. *gaspensis* Fern. | Sedge | WL | |
| *C. hassei* Bailey (= *C. garberi* var. *bifaria*) | Garber's Sedge | WL | |
| Juncaceae | | | |
| *Juncus stygius* L. ssp. *americanus* (Buch.) Hulten | Moor Rush | SC | |
| *J. trifidus* L. | Rush | WL | |
| Iridaceae | | | |
| *Iris setosa* Pallas *ex* Link. var. *canadensis* M. Foster (= *I. hookeri*) | Beach-head Iris | WL | |
| Liliaceae | | | |
| *Allium canadense* L. | Wild Garlic | SC | |
| *A. tricoccum* Ait. | Wild Leek | WL | |
| *Tofieldia glutinosa* (Michx.) Pers. | False Asphodel | WL | |
| Orchidaceae | | | |
| *Arethusa bulbosa* L. | Arethusa | WL | |
| *Calypso bulbosa* (L.) Oakes | Fairy Slipper | WL | |
| *Listera auriculata* Wieg. | Auricled Tway-blade | SC | 2 |

Table 2. Continued.

| Scientific Name | Common Name | Status | |
|---|---|---|---|
| | | Maine | Federal |
| Poaceae | | | |
| *Agrostis mertensii* Trin. (= *A. borealis*) | Boreal Bentgrass | SC | |
| *Danthonia spicata* (L.) Beauv. *ex* Roemer & Schultes var. *pinetorum* Piper | White Oat-grass | WL | |
| Zannichelliaceae | | | |
| *Zannichellia palustris* L. | Horned Pondweed | SC | |

"known to be extinct," but formerly known populations have not been found extant. If any of the 90 Special Concern—Possibly Extirpated plant taxa is found, it will be listed as Endangered upon approval of documentation by the Critical Areas Program.

Special Concern includes plants with five to ten occurrences, for which some threat is indicated. *Betula* × *caerulea,* a fertile hybrid (DeHond and Campbell, 1989), has nine recent occurrences in Maine, and is at risk because of its value for timber. The Watch List is for plant taxa with more than 10 documented recent occurrences, and for which there is reason for concern. It includes varieties or subspecies qualifying for one of the other categories but belonging to species with more than ten recent occurrences in Maine, such as *Adiantum pedatum* var. *aleuticum, Danthonia spicata* var. *pinetorum,* and *Mimulus ringens* var. *colpophilus.* The Special Concern—Possibly Extirpated List, Special Concern List and Watch List are reviewed at least biennially.

Only native plants growing without cultivation are listed. Fernald (1950) is the source for determination of natural and indigenous occurrence. Taxonomic status and nomenclature primarily follow Kartesz and Kartesz (1980) and recent taxonomic changes (e.g., Greene, 1984). As field verifications, monitoring programs and research proceed, revisions to the Official List and administrative lists will be made at least biennially by the Maine Critical Areas Program with the assistance of the Endangered Plant Technical Advisory Committee.

The purpose of the Official List is to give the State of Maine an authoritative notification of Endangered and Threatened Plants. This list will be used by state government to establish conser-

vation priorities, to expedite its own environmental reviews, and to distribute to land use consultants and developers conducting site evaluations and preparing environmental impact statements. In addition, the Critical Areas Program will use the list for establishing priorities in landowner contact programs, for population monitoring and for developing conservation strategies.

## DISTRIBUTION AND COMPOSITION OF MAINE'S ENDANGERED AND THREATENED FLORA

The presence of southern and northern floristic elements in Maine accounts for much of the state's rare flora. On one hand, of the 159 Endangered and Threatened plants, 37 percent reach the northern limit of their range in Maine. Twenty-eight percent occur in the southwestern corner of the state (York and Cumberland Counties) where generally small peripheral or disjunct populations represent species that are usually more common further south. Examples of this southern element are *Cornus florida*, *Liatris scariosa* var. *novae-angliae* (*L. borealis*), *Rhododendron maximum*, and *Quercus montana* (*Q. prinus*) (Eastman, 1976a, 1976b; Tyler and Gawler, 1980). On the other hand, forty-two percent of the 159 Endangered and Threatened plants reach the southern limit of their range in the state. These include many arctic/alpine and boreal peatland species which are found at high elevations in Maine (May and Davis, 1978), along the northeastern coast (Worley, 1980; Olday et al., 1983), and in unusual habitats such as calcareous fens (Davis and Sawyer, 1978; Rooney et al., 1979).

Rare plant areas of major importance in Maine include Mt. Katahdin (elev. 5267 ft./1605 m) with its diverse alpine flora (Hudson, 1988), including 23 Endangered, 10 Threatened, and four Special Concern—Possibly Extirpated taxa; the St. John River valley with *Pedicularis furbishiae* and four other Endangered, six Threatened and two Special Concern—Possibly Extirpated plants (Richards, 1980; Gawler, 1983; Menges and Gawler, 1986); Crystal Bog, a rich fen in northern Maine with three Endangered, two Threatened and one Special Concern—Possibly Extirpated taxa (Davis and Sawyer, 1978; Rooney et al., 1979; Eastman, 1981); and Twin Peaks (Campbell and Eastman, 1978; Tyler and Gawler, 1980) where one Endangered and eight Threatened taxa occur.

The composition of Maine's list of Endangered and Threatened plants could be of use in unravelling some factors in plant species rarity and endangerment, such as dispersal patterns or restricted habitat (Drury, 1980). Scarcity of calcareous bedrock exposures in Maine preadapts calcicoles for rarity; one-third of Maine's Endangered and Threatened plants are calcicoles (Critical Areas Program, 1985a). The percent herbaceous (versus woody) plants is the same (82 percent) in both the combined Endangered and Threatened categories of the Official List and in Maine's total native flora (Richards et al., 1983). Seven percent are ferns and fern allies, though this group comprises only five percent of the native flora. Twenty-two percent of Maine's Endangered and Threatened plants occur in arctic/alpine habitats, and 12 percent are associated with a riverine habitat or are restricted to river valleys. Eight percent are aquatics, eight percent are peatland plants, and eight percent are salt marsh plants. Of all families in the List, the Cyperaceae contains the highest number of Endangered and Threatened species (18), with 15 species of *Carex*; this number is 10 percent of all Maine's Endangered and Threatened taxa, the same percentage as the genus represents in Maine's native flora. Other families prominently represented in the Endangered and Threatened categories of the List are the Poaceae (14 species), Asteraceae (13 species), Orchidaceae (11 species), Ericaceae (7 species), Salicaceae (6 species), and Brassicaceae (6 species).

Unlike California, where 47 percent of the native flora are endemics (Elias, 1987), Maine has only one taxon, *Carex oronensis,* not known to occur outside the State. Plant taxa found in Maine and not elsewhere in the contiguous United States are *Agalinis neoscotica, Oxytropis campestris* var. *johannensis, Pedicularis furbishiae, Salix arctophila* and *Saxifraga foliolosa* var. *foliolosa* (*S. stellaris* var. *comosa*). Found in Maine but not elsewhere in New England are *Drosera anglica, Drosera linearis, Epilobium anagallidifolium, Juncus stygius* var. *americanus, Mimulus ringens* var. *colpophilus, Platanthera* (*Habenaria*) *leucophaea, Ranunculus lapponicus, Salix exigua* (*S. interior* var. *exterior*), and *Selaginella selaginoides* (Crow et al., 1981; Crow, 1982; Critical Areas Program, 1985a).

Maine's Official List will serve as a valuable tool in conservation education, as a guide for implementing conservation programs, and as a stimulus to plant biologists to locate new occurrences or

re-locate historical occurrences of these rare plants. The Critical Areas Program notifies and corresponds with landowners if such plants are located. It is hoped that botanists throughout the northeast will examine the list of 90 Special Concern—Possibly Extirpated plants and join in the effort to re-locate in Maine such rarities as *Juncus subtilis, Polygala cruciata, Galium obtusum, Silene acaulis* var. *acaulis, Gentianella quinquefolia* and *Carex rariflora.*

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# BY-LAWS
# OF
# THE NEW ENGLAND BOTANICAL CLUB, INCORPORATED

(To repeal and replace all previous By-Laws)

## ARTICLE I
### NAME AND PURPOSE

Section 1. The name of this corporation shall be The New England Botanical Club, Incorporated.

Section 2. Its purpose shall be to promote the dissemination of local and general botanical information.

Section 3. The Club shall be organized and operated exclusively for its educational and scientific purposes. No part of the property or net earnings of the Club shall inure to the benefit of any individual; and no part of the property of the Club shall be used directly or indirectly in carrying on propaganda, nor shall any substantial part of the activities of the Club consist of the carrying on of propaganda or otherwise attempting to influence legislation. The Club shall not participate in, nor intervene in, any political campaign on behalf of any candidate for public office, nor shall it publish or distribute any statements with respect thereto.

## ARTICLE II
### SEAL

The seal of the Club shall, subject to alteration by the Council, consist of a flat-faced circular die with the words "Massachusetts," "Organized 1895, Incorporated 1920" and the name of the corporation cut or engraved thereon.

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Adopted by the membership April 7, 1989

By-Laws last published: Rhodora 81: 275–281 (1979)

## ARTICLE III

### OFFICERS

Section 1. The officers of the Club shall be a President, a Vice-President, a Curator of Vascular Plants, an Assistant Curator of Vascular Plants, a Curator of Nonvascular Plants, a Librarian, a Corresponding Secretary, a Recording Secretary, a Treasurer, and five councillors—one of whom may be a student and one of whom may be the immediately preceding President. The Council shall appoint annually an Associate Curator to serve as a liaison with the Harvard University Herbaria. The Council shall consist of the above-named Officers, the Councillors, the Associate Curator, the Program Chairman, and the Editor-in-Chief of *Rhodora*.

Section 2. All officers shall be elected by ballot by a majority of those members voting at the annual meeting of the Club, and, except in the case of death, resignation, or removal, each officer shall hold office until the next annual meeting or until a successor is elected. Voting by proxy shall not be allowed.

Section 3. If the office of any officer becomes vacant by reason of death, resignation, or removal, the Council may appoint a successor who shall hold office until the next annual meeting or until a successor is elected.

## ARTICLE IV
### COUNCIL

Section 1. The Council, six members of which shall constitute a quorum, shall have the management and control of the Club and of all its property and affairs and shall direct the expenditure of its funds.

Section 2. The Council shall authorize and approve, except as the Council may generally or in particular cases authorize the execution thereof in some other manner, all deeds, transfers, and contracts; and all bonds or notes made or endorsed by the Club shall be signed by the Treasurer and countersigned by the President or the Vice-President. All deeds, transfers, and contracts shall be signed by the President or in the President's absence by the Vice-President.

Section 3. The Council may appoint and remove such other officers or agents as it may from time to time determine. It may appoint committees as it sees fit and may delegate to these committees such powers for such terms as the Council deems best, subject to the power of the Council to revoke any such appointment at any time.

Section 4. The Council shall have the books and accounts of the Treasurer audited at least once a year by an external Auditor.

## ARTICLE V
### DUTIES OF OFFICERS

Section 1. The President and Vice-President shall perform the usual duties of their offices.

Section 2. The Curator of Vascular Plants and the Curator of Nonvascular Plants shall have charge of the botanical collections of the Club. The Assistant Curator of Vascular Plants (or in that officer's absence, the Associate Curator) shall perform the duties of the Curator of Vascular Plants in the Curator's absence.

Section 3. The Librarian shall have charge of the books and manuscripts of the Club.

Section 4. The Corresponding Secretary shall give notices of

all meetings of the Club and of the Council, shall conduct the correspondence of the Club, and shall notify all persons elected to membership or to office of their election.

Section **5**. The Recording Secretary, who shall be the Clerk, shall be sworn before entering upon the duties of the Recording Secretary, and as such shall keep the minutes of all meetings of the Club and of the Council and such other records as the Council may direct.

Section **6**. The Treasurer shall, subject to the orders and supervision of the Council, collect and disburse the funds of the Club, and for this purpose shall have power to endorse for deposit or collection, all funds, checks, drafts, etc., payable to the corporation or its order. The Treasurer shall keep, or cause to be kept, accurate books of account, and shall make a report of the financial condition of the Club at each annual meeting, and at such other times as the Council may request.

## ARTICLE VI
### NOMINATING COMMITTEE

On or before December fifteenth of each year, the President shall appoint a committee of three members—who shall not be officers—to nominate officers for the ensuing year. The report of this committee, which shall be filed with the Corresponding Secretary and open to inspection at least three weeks prior to the annual meeting, shall be incorporated in the call for the annual meeting.

Nothing herein shall restrict the right of members to offer nominations from the floor provided a notice listing such nominees and signed by not less than three members shall be filed with the Corresponding Secretary not later than ten days prior to the date of the meeting.

## ARTICLE VII
### MEMBERSHIP AND DUES

All members shall have voting privileges and shall receive *Rhodora*. Dues and subscription price of *Rhodora* shall be determined at appropriate intervals by the Council. Annual dues shall be payable the first of January.

## ARTICLE VIII

### ELECTION TO MEMBERSHIP

Section 1. Application for membership shall be made in writing to the Club and presented by the Corresponding Secretary to the Council for endorsement at its next meeting. Favorable action by the Council on any such application shall constitute a recommendation of the applicant, whose name shall then be placed before the Club for election at any regular meeting of the Club. Notice of election to membership shall be printed in the subsequent Club meeting notice.

Section 2. All elections to membership shall be by a simple majority vote at any regular meeting of the Club.

Section 3. Persons elected to membership shall, within thirty days after receiving notice of election, accept said election by paying the Club dues. Failure by any person elected to membership to comply with this provision shall render such election void.

## ARTICLE IX

### TERMINATION OF MEMBERSHIP

Section 1. Resignations of membership may be made in writing to the Corresponding Secretary.

Section 2. Any member whose dues remain unpaid for more than three months after same become payable shall cease to receive *Rhodora*. The membership of any member shall automatically terminate if dues or other indebtedness to the Club remain unpaid for thirteen months after same become payable.

Section 3. The Council may, by a two-thirds vote of its entire number, after notice and opportunity for hearing, suspend or expel any member.

Section 4. In the event of the death, resignation, or other termination of the membership of a member, all privileges shall cease.

## ARTICLE X

### MEETINGS OF THE CLUB

Section 1. The Annual Meeting of the Club shall be held on the first Friday in March of each year, unless otherwise ordered

by the Council, and regular meetings shall be held monthly, except during July, August and September at such times as the Council may determine. If the Annual Meeting is omitted by oversight or otherwise on the day herein provided therefor, a special meeting may be held in place thereof, and any business transacted or elections held at such meeting shall have the same effect as though transacted or held at the annual meeting.

Section 2. Special meetings may be called by the President or by vote of the Council or by written request of any ten members given to the Corresponding Secretary. Every such call shall state the object for which the meeting is called.

Section 3. Notice of all meetings shall be distributed at least seven days before such meetings.

Section 4. At any meeting of the Club, fifteen members shall constitute a quorum for the transaction of business, except the amendment of the By-Laws.

## ARTICLE XI
### AMENDMENTS OF BY-LAWS

These By-Laws may be altered, amended, or repealed in the following manner: at any annual, regular, or special meeting of the Club by a two-thirds vote of the members present and voting, provided that at least thirty members or two-thirds of the membership (whichever is the smaller number) are present at the meeting, and that the subject matter of the proposed alteration, amendment, or repeal has been given in the call for the meeting at which the alteration, amendment, or repeal is to be considered.

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THE NEW ENGLAND BOTANICAL CLUB
22 Divinity Avenue
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# Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB

Vol. 91 October 1989 No. 868

# The New England Botanical Club, Inc.

22 Divinity Avenue, Cambridge, Massachusetts 02138

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**Cover Illustration**

*Agalinis acuta* Pennell (Sand-Plain Gerardia). A very rare plant of the coastal plain in danger of extinction; known only from Cape Cod and Long Island. Recently listed by the U.S. Fish & Wildlife as Threatened. Original artwork by Tess Feltes: from *New England's Rare, Threatened and Endangered Plants*. Crow, G. E. 1982. Reproduced by permission.

# Rhodora

JOURNAL OF THE
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RHODORA, Vol. 91, No. 868, pp. 279–281, 1989


## *VACCINIUM SEMPERVIRENS* RAF.: A LOST SYNONYM FOR *VACCINIUM OVATUM* PURSH[1]


W. Benson Kirkman


*Vaccinium sempervirens* Rayner & Henderson (1980) was proposed in 1980 as a new species in *Vaccinium* section *Herpothamnus* (Small) Sleumer. This section was previously recognized as monotypic, consisting only of *V. crassifolium* Andrews (1800). As a result of their study of sect. *Herpothamnus,* Kirkman and Ballington have suggested that *V. sempervirens* be reduced to a subspecies of *V. crassifolium* (Kirkman, 1987, Ph.D. dissertation, N. Carolina State Univ., Raleigh; Kirkman and Ballington, 1989; Kirkman et al., 1989).

While researching the taxonomic history of sect. *Herpothamnus,* a previous use of the binomial *Vaccinium sempervirens* by C. S. Rafinesque was discovered in Merrill's (1949) *Index Rafinesquianus:* "*V. sempervirens* Raf. Herb. Raf. 54. 1833, *nom.* Oregon (Lewis and Clark)." Merrill's use of "*nomen*" indicated that Rafinesque's publication listed the name without a description. However, the fact that Merrill did not say "*nomen nudum*" led me to a more extensive search of Rafinesque's work.

Rafinesque (1833) indicated that he had established *Vaccinium sempervirens* in his "Mpt florula 1817," leading to a search for that publication, and subsequently to consultation with the historian Charles Boewe. Boewe recognized that "Mpt" was an abbreviation for "manuscript" and concluded that Rafinesque was referring to his *Florula Missurica, Mandanensis and Oregonensis,* a "pamphlet" he listed for 1817 on page 35 of his *Herbarium Rafinesquianum* (1833). Rafinesque wrote out a manuscript for

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[1] Paper No. 11102 of the Journal Series of the North Carolina Agricultural Research Service, Raleigh, NC 27695-7601.





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this "pamphlet" at least twice, sending it to William Swainson for publication in England and to Bory de Saint-Vincent in Brussels for publication in the *Annales Générales des Sciences Physiques*; but it never was published, and is not among the Swainson papers at the Linnean Society of London. Boewe also unsuccessfully searched Rafinesque's letters of the period, especially those to A. P. de Candolle, because Rafinesque frequently sent substantial plant descriptions to Candolle, hoping they would appear in the latter's *Prodromus*.

The last chance in Boewe's search for Rafinesque's *Vaccinium sempervirens* was an unpublished Rafinesque manuscript from the period located in the American Philosophical Society Library in Philadelphia. Its title had been listed as "*Neophyton; or new plants, genera and species from North Carolina,* by C. S. Rafinesque. Book first, Philadelphia 1830 (300 numbers)." Boewe later checked the manuscript in Philadelphia and found that "North Carolina" was actually "North America." The first book (of three), contained the following entry as transcribed from Rafinesque's handwriting by Boewe:

> "283 Vaccinium sempervirens Raf. [(]1816) fol. perennis petiolatis ovato oblongis, acutis, serrulatis, plicatis, coriaceis, lucidis subtus glaucis, Baccis pendulis atropurpureis—In Oregon 6 to 8 feet high. Berries dried by Ind[ians], or baked, cakes or bread of it."

There is no doubt that Rafinesque was describing *V. ovatum* Pursh which was published in Pursh's *Flora Americae septentrionalis* (1814), and "Oregon" was the territory in the Pacific Northwest. Rafinesque was aware of *V. ovatum,* since he published the only review of Pursh's book to appear in Pursh's lifetime (Rafinesque, 1818). The only mention of *Vaccinium* in that review, however, is of what is now *V. stamineum* L., which he referred to as forming "a peculiar genus or subgenus, *Polycodium.*" He further suggested that "the whole tribe of *Ericacea* or *Bicornia* must be newly modelled."

Although Rafinesque apparently tried to publish a description of *Vaccinium sempervirens* at least three times, until now only the name and proposed location of the description have been published. A specimen has not been found, even among the Rafinesque specimens recently uncovered by W. R. Overlease (1986, pers. comm.) in William Darlington's herbarium at West Chester University. The specimen was probably among those in Rafinesque's personal herbarium that were purged by Elias Durand or

destroyed by rats following Rafinesque's death (Merrill, 1949; Stuckey, 1971). Since the name is a *nomen nudum,* there can be no effect on the validity of *V. ovatum* or the later use of *V. sempervirens* by Rayner and Henderson. However, in light of the evidence presented, there is a case for recognizing *V. sempervirens* Raf. Herb. Raf. 54. 1833. *nom. nud.* as a synonym for *V. ovatum.*

## ACKNOWLEDGMENTS

The author expresses special appreciation to Dr. Charles Boewe, Research Associate at the Filson Club in Louisville, Kentucky, for locating and transcribing the description of *Vaccinium sempervirens* Raf. and for reviewing the manuscript.

The author also thanks Mrs. Judy Ho of Special Collections at the National Agricultural Library, Beltsville, Maryland, for her assistance and encouragement in researching the taxonomic history of *Vaccinium* section *Herpothamnus.*

Finally, the author thanks Drs. J. R. Ballington and J. W. Hardin of North Carolina State University for their support throughout this project and for reviews of the manuscript.

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# *GAULTHERIA PROCUMBENS* AT PINE HILLS, INDIANA—ITS CONTINUED DECLINE AND INCIPIENT EXTIRPATION, 1951–1981

DANIEL B. WARD

## ABSTRACT

Wintergreen, *Gaultheria procumbens,* a perennial evergreen member of the boreal forest, has persisted as a post-glacial relic on an acidic, south-facing slope at Pine Hills, Montgomery County, Indiana. The population area is believed to have been minimal in 1868 when overlying hemlock was cut. Surveys in 1951, 1961, 1971, and 1981 have shown the colonies to have expanded vigorously until 1961, then to have undergone a precipitous collapse, associated with regrowth of the hemlock, and to have now approached local extinction. An effort to reverse the population decline by removal of a portion of the hemlock overstory appears not to have been successful.

Key Words: *Gaultheria procumbens, Tsuga canadensis,* glacial relic, extinction, Pine Hills, Indiana

## INTRODUCTION

In the centuries following the Glacial Maximum, 18,000 Y.B.P., the zones of vegetation forced southward by the advance of the ice returned northward, each in turn overriding and displacing the more cold-resistant floras, but occasionally leaving pockets of boreal species in favorable niches.

*Gaultheria procumbens* L., or wintergreen, was one of the species so isolated (Friesner, 1937). In Indiana it has survived in only five counties south of the northern third of the state (Deam, 1940). In the first discovered (Coulter, 1900) and most carefully monitored (Ward, 1976) of these stations, a population in the Pine Hills Natural Area of Montgomery County, the species has been observed over a recent 30 year period to have undergone a rapid decline in numbers and vigor, and to have now approached local extinction. The previous local abundance of wintergreen is thought to be a result of removal of the hemlock overstory in 1868, and its recent near-disappearance is believed caused by forest regrowth.

This study continues a project begun in 1951 of surveying and mapping *Gaultheria* as it occurs in the Pine Hills area, to deter-

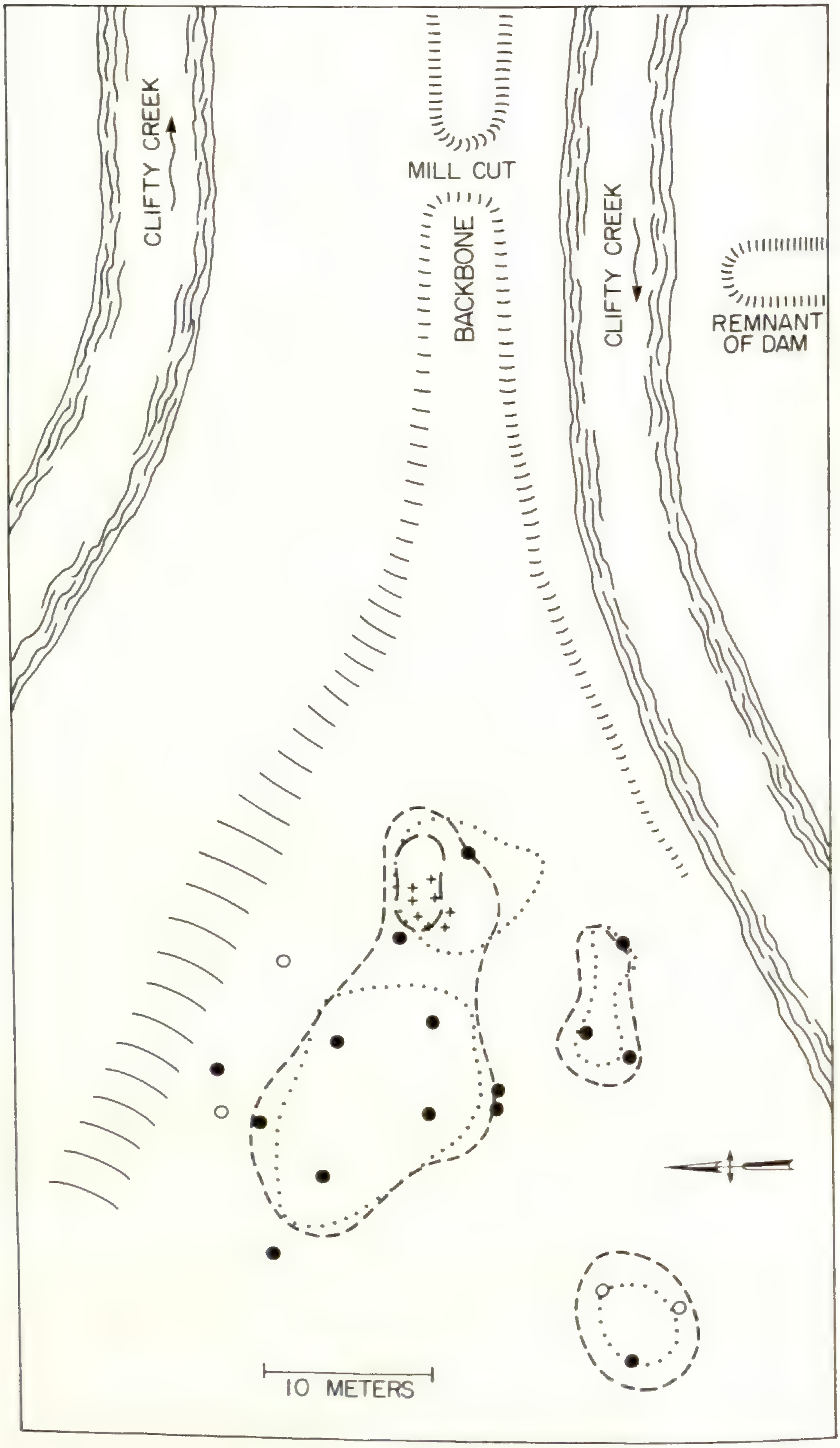
mine the factors affecting its survival and decline. The present paper recapitulates the observations and interpretations obtained by surveys in 1951, 1961, and 1971 (Ward, 1976), and extends these observations to include a survey conducted in 1981 and subsequent efforts to preserve the population.

## THE PINE HILLS AREA

The Pine Hills Natural Area, in southwestern Montgomery County, Indiana, is an oft-studied region of steep cliffs, cool north-facing slopes, and well-leached acid ridges. The physiography has been described by Smith (1933), the vegetation has been mapped by Friesner and Potzger (1934), the soil acidity and its relation to hemlock reproduction has been examined by Potzger and Friesner (1937), and the flora has been inventoried by McCormick (1962). Its significance as a natural area is such that it was appropriately given a rating of "1" by Lindsey et al. (1969). By the happenstance of prolonged single-family ownership and pride in its natural features, the Pine Hills central area survived without significant disturbance until funds were available for completion of its purchase by The Nature Conservancy in 1960 (McCormick, 1962). It is now assigned for maintenance in perpetuity as a wilderness area by the State of Indiana, administered by the Indiana Department of Natural Resources.

Pine Hills is most noted for an impressive series of incised meanders of Indian Creek and its subsidiary Clifty Creek, tributaries of Sugar Creek, the principal drainage channel of the region. During the Pleistocene glacial cycles, morainal deposition displaced Sugar Creek from its original channel and forced it into a new alignment closer to the headwaters of Indian and Clifty Creeks, thus steepening the gradient of these lateral streams. Subsequent erosion of the underlying sandstones has deeply entrenched both Sugar Creek and its tributaries, while retaining the meandering course that these secondary streams had established in the mature pre-glacial topography.

At seven places in the Pine Hills area these streams bend back upon themselves, or upon each other, to form steep-sided ridges or "backbones" up to 70 m long and 33 m above the stream beds (Smith, 1933). The backbone known as "Mill Cut" is formed by a looping bend of Clifty Creek. This stream in its headwaters


CLIFTY CREEK
MILL CUT
BACKBONE
CLIFTY CREEK
REMNANT
OF DAM
10 METERS

flows generally northward, abruptly changes direction to the west, circles widely to the north and east, and approaches the course of its westward channel before again turning sharply northward, eventually to join Indian Creek (Figure 1). The westward and eastward legs of the stream thus flow in opposite directions but in close proximity, separated by a sheer two-faced wall of Borden sandstone.

This wall, the Mill Cut Backbone, has been formed in the same manner as the other backbones of the Pine Hills region (Smith, 1933). The Borden deposits, of Middle Mississippian age, are subject to frost action parallel to the exposure surface and independent of the essentially horizontal bedding planes, the rock spalling off in great flakes up to a meter or more in width. The erosive effect of repeated freeze-and-spall, with the debris periodically removed by streamflow storm surges, has produced a channel that varies in depth from 9 or 10 m at the lowest point of the backbone to over 20 m at the east end where the backbone merges with the adjacent upland.

The history of human activity in the vicinity of the backbone has been recovered in part by McCormick (1962) from historic papers and census records. A contract was signed December 4, 1868 permitting the construction of a dam on Clifty Creek for the purpose of supplying water power to machinery, and the enterprise was incorporated as the Pine Hill Woolen Mill Company. In the winter of 1868–69, a rough roadway was graded down the ravine slope of Clifty Creek to the south of the backbone and a log crib and rock-rubble dam 4.6 m high was constructed across the stream. The cribbing of this dam was primarily of hemlock logs cut from the adjacent south-facing slope, immediately west of the backbone. A square-bottomed notch or "millcut," about

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←

Figure 1. Map showing Mill Cut Backbone, Pine Hills, Indiana, and associated colonies of *Gaultheria procumbens*. Clifty Creek flows from upper right, downward along the south face of the backbone, then circles widely (off the plate) to reappear on the north face of the backbone. Within this loop of Clifty Creek a knoll (indicated by hatch lines) extends eastward to a cut where a millrace was located in 1868. The dam which once blocked the stream remains only as a low mound of rock rubble. Major trees are indicated by large dots (with those dead since 1951 represented by hollow dots). The colonies of *Gaultheria* present in 1951 are represented by perimeters of small dots, those in 1961 by short dashes, and those in 1971 by long dashes. Plants surviving in 1981 are shown by crosses (+).

6 m deep and 3 m wide, reaching to within 3 m of the bed of the west-flowing channel, was cut through the narrowest and lowest portion of the backbone, and a wooden flume from the north side of the notch carried the impounded waters about 50 m to an overshot waterwheel at a small, 208 spindle woolen mill that was located on the terrace of Clifty Creek to the north of the backbone.

Perhaps because of the unstable and often destructive force of the stream, in 1873 one of the original investors built a new, larger mill on Sugar Creek below the mouth of Indian Creek (Kennedy, 1881), and the small mill on Clifty Creek was abandoned. Today only a low mound outlining the southern end of the dam, a remnant of the access road, and the prominent millcut, give an overt indication of this brief industrial activity. Yet the changes observed over recent decades in the area covered by wintergreen on the knoll at the west end of the backbone can be explained only as collateral consequences of this human disturbance more than a century ago.

In historic times, *Gaultheria procumbens* in the Pine Hills region has been known only on the knoll encircled by the loop of Clifty Creek as it swings from the south to the north side of the Mill Cut Backbone (Figure 1). As the creek entrenched itself in the Borden formation it swung ever wider in the westward portion of its bend, leaving an elevated rise surrounded on the south, west, and north by the stream and connected to the upland to the east only by the narrow ridge of the backbone. Through time, the circumneutral glacial overburden of this knoll was removed by erosion, leaving a thin acidic soil derived from the parent Borden sandstone. The surface of the knoll slopes downward to the south, smoothly merging with a narrow bench just above the west-flowing leg of the stream. It is on this gradual south-facing slope that *Gaultheria,* following its post-Pleistocene re-establishment in north-central Indiana, has long persisted.

## PREVIOUS STUDIES

The Mill Cut Backbone stand of wintergreen has been known to the writer since his boyhood in the early 1940's while on recreational outings and field trips with Dr. Albert R. Bechtel, professor of botany at Wabash College and a family friend. In those early years the Mill Cut knoll was an open, well-lit slope,

free of significant undergrowth, and the *Gaultheria* was conspicuous as dense, sharply defined, evergreen carpets. Tiny hemlock seedlings protruded here and there, adding charm to the scene and in no way suggesting the devastation to the wintergreen that their continued growth would ultimately bring.

In 1951, the writer, then in graduate school and aware of the relic importance of the *Gaultheria* stand, began a series of periodic plant surveys of the Mill Cut knoll. The observations made in 1951, 1961, and 1971 were summarized and published in 1976 (Ward, 1976).

In August, 1981, a fourth decennial survey was conducted. As in the previous surveys, the larger trees on the site were used as reference points, thus permitting precise location of the surviving *Gaultheria*.

## RESULTS

The vegetation of the *Gaultheria* slope and its changes over the first twenty years of this study have been described in some detail (Ward, 1976). The slope was originally sparsely covered with mature trees. Toward the crest, northern red oak (*Quercus rubra* L.), black oak (*Q. velutina* Lam.), and a few large hemlocks (*Tsuga canadensis* (L.) Carr.) were predominant, while lower on the slope white oak (*Q. alba* L.) and white pine (*Pinus strobus* L.) appeared. The understory near the crest was formed of black gum (*Nyssa sylvatica* Marsh.), flowering dogwood (*Cornus florida* L.), red cedar (*Juniperus virginiana* L.), witchhazel (*Hamamelis virginiana* L.), and wild hydrangea (*Hydrangea arborescens* L.). These were replaced lower on the slope by shadblow (*Amelanchier arborea* (Michx. f.) Fern.), ironwood (*Ostrya virginiana* (Mill.) K. Koch), red maple (*Acer rubrum* L.), mapleleaf viburnum (*Viburnum acerifolium* L.), sassafras (*Sassafras albidum* (Nutt.) Nees), partridgeberry (*Mitchella repens* L.), and running euonymus (*Euonymus obovatus* Nutt.). Wintergreen (*Gaultheria procumbens*) was restricted to this slope, below the crest and above the stream bench of Clifty Creek, where it formed dense mats or colonies of low, perennial, vegetatively reproducing, woody stems.

The appearance of the *Gaultheria* slope had changed markedly during the first 20 years it was under observation (Ward, 1976). In 1951 the area was sunny and open, but to some extent by 1961

and conspicuously by 1971 had become thickly covered with sapling hemlocks plus a smaller number of young white pines. By the fourth decennial survey, in 1981, these young trees were 3–6 m tall with basal diameters ca. 5 cm. All lower branches were dead, as were many of the smaller trees, a probable consequence of crowding and shading. In most parts of the area there was little opportunity for the lower vegetation layers to receive direct sunlight, while in the more open places perhaps 5–15% of the ground surface was lit by the noonday sun.

The area covered by *Gaultheria* in the four decennial surveys documents the initial expansion and subsequent collapse of the population. The 1951 observations recorded wintergreen in four distinct and sharply demarked colonies (Figure 1). These ranged in area from 16 $m^2$ to 130 $m^2$, and together covered 204 $m^2$. An estimated 100 stems/$m^2$ were present in most areas. By 1961 each of the four colonies was slightly enlarged, two of them having met and become one, with a total area of 307 $m^2$. The maximum distance *Gaultheria* was found outside the 1951 perimeter was approximately 150 cm, suggesting an average annual rate of spread of 10 to 15 cm. Although the colonies remained vigorous, their future decline was adumbrated by a reduced density with no areas appearing to exceed 80 stems/$m^2$ and small portions supporting few or no plants. By 1971 the colonies had lost their discrete outlines. One of the colonies no longer existed, a second was represented by two plants, while the formerly merged colony was reduced to 16.3 $m^2$, containing no more than 5 to 10 leaf-bearing stems/$m^2$, plus some 21 scattered, single-stemmed plants.

By 1981 the wintergreen had very nearly disappeared. Initially only two plants were found, but on a subsequent inspection a total of 8 plants was located, all in or near the area that had been most densely covered at the time of the previous survey. Each plant was represented by a single upright stem. The typical *Gaultheria* pattern of alternate leaves in which three or four adjacent nodes are suppressed, thus giving the appearance of annual whorls, had given way to two pairs of leaves, the upper pair much smaller than the two formed the previous season.

These changes in population size and vigor were measured in the four decennial surveys by careful mapping and calculation of the area covered, by counts of individual, isolated plants, and by estimates of the number of stems/$m^2$. This last measure, of stem density, is unquestionably of importance in measuring the vigor

of the colony and may serve well as a harbinger of future population expansions or declines, but is not retrospectively quantifiable. Thus, area covered by the population, supplemented by token values given to remnant fragments, seems to provide the best available measure of population size.

In addition to the values obtained in the four decennial surveys from 1951 through 1981, a population estimate is available for 1868, when the *Gaultheria* slope was logged and light intensity at the understory level was increased. Since the vigorous growth observed between 1951 and 1961 could not have been of long duration without having completely covered the Mill Cut knoll, the four colonies initially observed may have been derived from as few as four plants surviving when the overlying timber was removed in 1868. No reproduction by seed was observed, either within the perimeter of the colonies or elsewhere on the knoll.

The area covered by the *Gaultheria* colonies in each of the decennial surveys, and the estimated minimal population size that may have been present in 1868, were plotted against time, to give a graphic representation of the apparent pattern of population expansion and collapse (Figure 2).

## DISCUSSION

A change in the area covered by *Gaultheria procumbens* at Pine Hills is a function of the temporary disequilibrium of the relationship between the plant and its environment. The vigor of the population as observed in 1951 and its continued growth through 1961 is a clear measure of conditions that favored expansion of the colonies. The most apparent factor permitting this expansion was an increased light intensity following the removal in 1868 of the overlying hemlock shade. Similarly, the deterioration of the population as measured in 1971 and its collapse by 1981 is an unmistakable consequence of a change in the previous advantageous condition, in the form of a dense, light-excluding growth of young hemlocks.

The Pine Hills *Gaultheria* population between 1868, when the assumed population size was minimal, and 1961 when a total area of 307 $m^2$ was recorded, conforms to an exponential rate of increase (Figure 2). This pattern of exponential increase is familiar in situations where carrying capacity of the environment is not

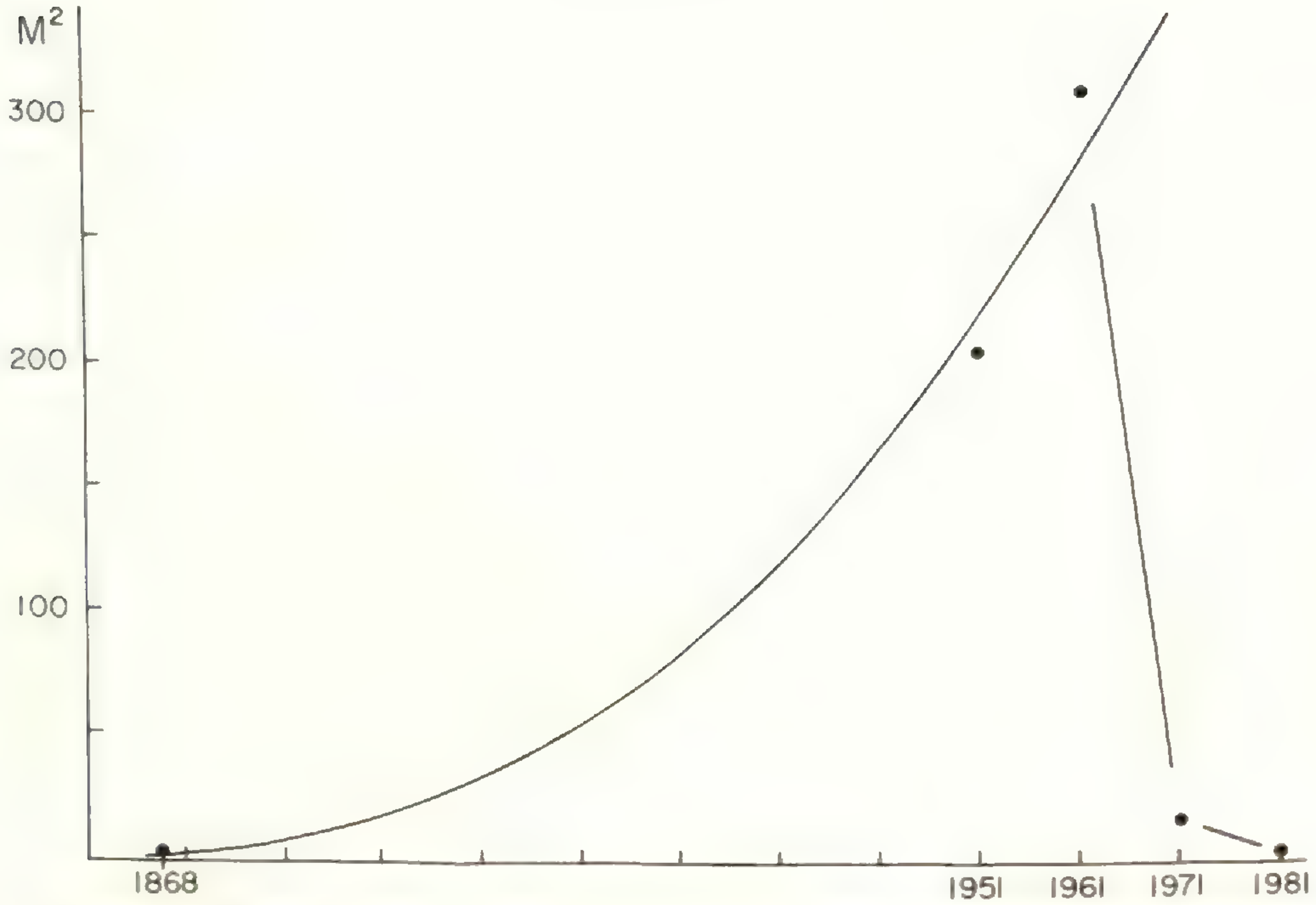


Figure 2. Growth curve showing the area occupied by *Gaultheria procumbens* colonies on the Mill Cut Backbone, Pine Hills, Indiana, in 1868 (estimated), 1951, 1961, 1971, and 1981. Change in the area of the colonies through 1961 approximates an exponential increase (line: $y = x^2$). Between 1961 and 1971, and continuing through 1981, the area of the colonies declined precipitously, to approach local extinction.

reached. There is no indication of the beginning of the familiar sigmoid curve or logistic in which factors limiting growth progressively come into play (Hutchinson, 1978; Silvertown, 1987).

The decline in population area between 1961 and 1981, though it had been foreshadowed by a thinning of stem density, was abrupt and not anticipated by observed transitional stages. The data permit only approximate straight-line indications of intermediate population size.

This pattern of vigorous growth followed by sudden collapse, without carrying capacity of the environment having been reached, is commonly experienced with populations of small short-lived organisms or organisms occupying transient habitats (Keeton, 1976), but has perhaps not previously been recorded in a population of perennial plants over an extended period of time.

The writer has examined in some detail the factors associated with the near-disappearance of *Gaultheria procumbens* from the Pine Hills area (Ward, 1976). The underlying Borden sandstone upon decomposition yields an acid soil that appears to be nec-

essary for the persistence of hemlock and white pine (Potzger and Friesner, 1937) and very possibly *Gaultheria*. The predominance of hemlock on the slopes of the various backbones of the Pine Hills, and particularly on the knolls which rise at the ends of these backbones within the loop of the encircling stream (Friesner and Potzger, 1934), together with the recent vigorous growth of hemlock on the Mill Cut knoll, at first suggested that this species is the expected climax on the wintergreen slope. The present restriction of mature hemlock to the crest of the knoll above the *Gaultheria* population was interpreted as the result of the removal in 1868 of these readily accessible, easily felled and shaped, mature trees from the lower slope, to form the log crib dam across Clifty Creek. Yet the infrequency with which *Gaultheria* is elsewhere associated with hemlock indicates that other species were surely a part of the arboreous flora.

*Gaultheria procumbens* is, as its common name clearly states, "winter green." This characteristic is presumably of value in permitting the plant to continue to photosynthesize during favorable weather in the late fall, winter, and early spring, when other species are leafless in a predominantly deciduous woodland. *Gaultheria* is not unique in this capability. In Ohio, 287 species, representing about 16% of that state's herbaceous flowering plants, have been identified as "winter-green" (Beatley, 1956).

The "winter-green" species of Ohio were found to be numerous in oak associations, while the only flowering plant observed to remain green in hemlock communities was *Mitchella repens*. *Gaultheria* was restricted to oak–chestnut, oak–hickory, and oak–pine associations (Beatley, 1956). In Indiana also, wintergreen is commonly associated with oak (Deam, 1940). Throughout the survey period the Mill Cut slope has supported a number of white oak, as well as a few black oak and northern red oak, some of which were estimated in 1971 to have dates of "zero diameter" of 1704, 1815, 1821, 1832, 1854, and 1858 (Ward, 1976). It thus appears probable that the slope at the time of logging in 1868 was not wholly covered with a dense stand of hemlock, but with a mixed association of hemlock and oak.

Perhaps the nearest physiographic match to the Mill Cut knoll is the ridge and slope at the east end of the adjacent ridge to the north, Turkey Backbone (Smith, 1933). The hemlock on the knoll and adjoining stream terrace of Turkey Backbone is the most extensive found in the Pine Hills area (Friesner and Potzger,

1934), and is almost without admixture of oak or other arboreous species. Yet the Turkey Backbone hemlock is growing on either level or north-facing surfaces, quite unlike the warm, sunny, south-facing *Gaultheria* slope of the Mill Cut knoll.

The *Gaultheria* population in 1868 may be appraised as consisting of no more than four isolated, marginally surviving plants, released by the abrupt removal of the shade of the hemlock overstory to expand into the four discrete colonies observed in 1951 (Ward, 1976). This supposition is supported by the observed rate of expansion of the population between 1951 and 1961. Since no point in the 1951 colonies was more than 4.9 m from the periphery, by the smaller estimate of 10 cm/year, approximately 50 years would have been sufficient for development of the largest colony. This figure has been suggested to be within permissible limits of error of the 83 years that had elapsed since construction of the dam and logging of the *Gaultheria* slope (Ward, 1976).

The decennial surveys from 1951 through 1981 were observational, and it is possible to state only by deduction the forces that were responsible for the changes in the *Gaultheria* population. Within this limitation, the post-Pleistocene history of *Gaultheria procumbens* in the Pine Hills area may be outlined. Following the last glacial recession the boreal forest again moved northward. Wintergreen was perhaps abundant, or at least sufficiently frequent to sustain populations of insect or other pollen vectors and agents of seed dissemination. With increasing climate moderation and intrusion of more temperate species, the boreal forest became restricted to limited sites of suitable soil or shade or moisture. In the Pine Hills area, though hemlock, white pine, and other boreal species were well adapted to many sites, *Gaultheria* was restricted to a niche found only on the sunny, south-facing, acidic, oak-forested slope of the Mill Cut knoll, and disappeared, or was never present, on the cooler, level terraces or north-facing slopes dominated by hemlock. Sexual reproduction ceased, perhaps through the disappearance of a pollinator, and the wintergreen colonies expanded or contracted in synchrony with fluctuations of hemlock incursion onto the south-facing slope. Perhaps windthrow of mature hemlocks on the shallow soil periodically opened the canopy and permitted expansion of the wintergreen, and subsequent regrowth of the hemlock again reduced the size and vigor of the colonies. In the mid-nineteenth century the wintergreen population was at a low level, perhaps very near local extinction. But

in 1868, by the intervention of man and his need for straight, easily felled logs for the construction of a nearby dam, the hemlock was wholly removed, leaving only a thin oak overstory beneath which the wintergreen recovered. The population thrived, by 1961 reaching a level and vigor in excess of that attained in past fluctuations. The hemlock also returned, its seeds finding a suitable bed in the dense carpets of wintergreen, and the extent of the opening caused by the removal of the mature trees providing an unprecedented absence of competition. The profuse growth of sapling hemlocks created a dense shade beneath which the wintergreen colonies ceased to expand and began to fragment. By 1981 only a few *Gaultheria* plants were to be seen, and the survival of the colony, so fortuitously prolonged by the 1868 logging, was again in peril.

## EPILOGUE

Upon completion of the 1981 survey it was abundantly apparent that the factors causing the decline in *Gaultheria* on the Mill Cut knoll would inevitably result in the local extinction of the species if left unchecked. Regrowth of the hemlock on the slope cut in 1868 was accepted as the dominant influence in this decline. Although the presence of *Gaultheria procumbens* in the northern tier of counties has precluded its classification as an endangered or threatened species in Indiana (Aldrich et al., 1986), retention of the native population of wintergreen, as a part of the Pine Hills relic flora, seemed to be of high scientific worth and well within the commitment by the State of Indiana to preserve the land and its natural resources in perpetuity.

A proposal was made to the Indiana Department of Natural Resources, custodian of Pine Hills, that the sapling hemlocks and pines be cut from a circle of 5 m radius centered on the few surviving wintergreen plants. The concept of this proposal was accepted, and in February, 1983 the small trees were removed from a 3 × 3 m square with overhanging branches trimmed from adjacent larger trees. At that date 8 plants were still present. It was anticipated that the increased light intensity would permit the continued survival and re-establishment of the population.

This expectation appears not to have been realized. In September 1988 the Department again surveyed the *Gaultheria* slope.

No plants were found. The summer of 1988 had been one of severe, almost unprecedented drought, and the Mill Cut knoll was exceptionally dry. It is to be hoped that the *Gaultheria* may have survived as bare stems among the fallen leaves and in a favorable season be able to appear again in the flora of the Pine Hills.

## ACKNOWLEDGMENTS

Thirty-plus years of tramping the Pine Hills has permitted the writer to receive companionship and help from family members and friends spanning three generations. In addition to those acknowledged previously (Ward, 1976), I wish to thank my wife, Suzanne, and my son, Gordon, for their assistance with the 1981 survey and J. A. Bacone, Indiana Department of Natural Resources, and his staff for their efforts and concern in preserving the natural resources which they hold in trust.

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# CHROMOSOME NUMBER DETERMINATIONS IN FAM. COMPOSITAE, TRIBE ASTEREAE. III. ADDITIONAL COUNTS AND COMMENTS ON GENERIC LIMITS AND ANCESTRAL BASE NUMBERS

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AND MEREDITH A. LANE

## ABSTRACT

Chromosome numbers of 261 individuals representing 121 taxa and 4 interspecific hybrids from 25 genera are reported. The majority of the counts are for *Aster, Gutierrezia* and *Solidago.* Nearly all counts confirm previous reports for the taxa; some reports are first counts for a state or province. Over 100 counts are from populations in California. Included are first reports for the following taxa: *Aster laevis* var. *guadalupensis,* $2n = 48$; *Aster priceae,* $2n = 64$; *Aster reticulatus,* $2n = 9_{II}$; *Aster wasatchensis,* $2n = 18$; *Gutierrezia solbrigii,* $2n = 20_{II}$; *Heterotheca jonesii,* $2n = 9_{II}$; *Heterotheca rutteri,* $2n = 18$; and *Stephanodoria tomentella,* $2n = 6_{II}$.

Key Words: Compositae, Astereae, chromosome numbers, *Aster, Gutierrezia, Haplopappus, Heterotheca, Solidago, Stephanodoria*

## INTRODUCTION

Biosystematic studies are enhanced by knowledge of variation in chromosome number within and between taxa (Strother, 1972). Determining the distribution patterns of cytotypes requires numerous counts from the range of a taxon. Ideally, when a large number of counts from the entire range of a single species, or species complex, can be accumulated, a paper limited to that taxon is published (e.g., Semple and Chmielewski, 1985; Chmielewski and Semple, 1985). However, for most taxa a career is required to build such a data base, and therefore only a few counts for most taxa are reported at a time in order to make the information generally available. This is the third in a continuing series of miscellaneous chromosome number reports on Astereae by the first author's laboratory (Semple, 1985; Semple and Chmielewski, 1987).

## MATERIALS AND METHODS

Meiotic counts were made from pollen mother cells dissected from buds fixed in the field in 3:1 EtOH:acetic acid, and sub-

sequently stored under refrigeration in 70% EtOH. Mitotic counts were made from root tip cells taken from transplanted rootstocks or seedlings. Root tips were pretreated in 0.01% colchicine for 2–3 hr., fixed in Modified Carnoy's Fixative (4:3:1 chloroform: EtOH: acetic acid), and hydrolyzed in 1 N HCl for 30 min. at 60°C before squashing. Both meristematic root tips and anther sacs containing microsporocytes were squashed in 1% acetic orcein and chromosome counts were made from freshly prepared material. Permanent slides were made in most cases and remain in the possession of J.C.S. (following Semple et al., 1981) or M.A.L. (following Jackson, 1973).

Voucher specimens for all counts are deposited in WAT, TEX or COLO unless otherwise indicated in Table 1.

## RESULTS AND DISCUSSION

The chromosome numbers of 261 individuals representing 121 taxa and 4 interspecific hybrids from 25 genera are reported for the first time (Table 1). The majority of the reports are for three genera: *Aster* (88 counts, not including *Virgulaster* and *Virgulus*), *Gutierrezia* (41 counts), and *Solidago* (73 counts). Populations were sampled in five provinces and territories in Canada, 29 states in the United States, five states in Mexico, and one province in Argentina. More than 100 of the collections were from California. All but a few counts are consistent with previous reports for the taxa and therefore are presented without comment. For most taxa too few counts have been reported to justify discussion of cytotype distribution patterns. Some counts are first reports for the taxon from a particular state; e.g., *Aster pilosus* var. *pringlei* ($2n = 48$) and *Solidago flexicaulis* ($2n = 36$) from Wisconsin, and *Virgulus pratensis* ($2n = 10$) from Florida.

The following are first reports for the taxon: *Aster laevis* L. var. *guadalupensis* A. G. Jones, $2n = 48$ (two populations); *Aster priceae* Britt., $2n = 64$ (five populations); *Aster reticulatus* Pursh, $2n = 9_{II}$ (three populations ); *Aster wasatchensis* (M. E. Jones) Blake, $2n = 18$ (one population); *Gutierrezia solbrigii* Cabrera, $2n = 20_{II}$ (one population); *Heterotheca jonesii* (Blake) Welsh & Atwood, $2n = 9_{II}$ (one population); *Heterotheca rutteri* (Rothr. in Gray) Shinners, $2n = 18$ (one population); and *Stephanodoria tomentella* (Robinson) Greene, $2n = 6_{II}$ (four populations).

Table 1. Chromosome number determinations of Astereae from Canada and the United States (unless otherwise indicated from Mexico or Argentina), arranged alphabetically. Vouchers were collected by Semple & Heard unless otherwise indicated: *Bt* = L. Brouillet; *CC#* = C. C. Chinnappa et al. collection numbers; *Ch* = J. Chmielewski; *L* = M. A. Lane; *R* = G. Ringuis; *S* = J. Semple.

*Acamptopappus shockleyi* Gray. $2n = 9_{II}$. **Nevada.** Clark Co.: S of NV-157 on dirt rd. into Kyle Canyon, *L. 3063.*

*Aphanostephus skirrhobasis* (DC.) Trel. var. *skirrhobasis.* $2n = 3_{II}$. **Texas.** San Patricio Co.: TX-361 0.5 mi W of Ingleside, *S 596* (MO).

*Aster* subg. *Aster* ($x = 9$ sections and subsections)

*A. divaricatus* L. $2n = 18$. **New York.** Cattaraugus Co.: US-219 7.6 km N of Ellicottville, *S & R 7569.*

*A. integrifolius* Nutt. $2n = 18$. **California.** Mono Co.: CA-108 6.2 km W of Leavitt Meadow Campground, *8728-2.*

*A. macrophyllus* L. $2n = 72$. **Pennsylvania.** Clearfield Co.: US-219 ca. 5 mi. S of Burnside, *S & R 7673.* Elko Co.: US-219 S of Wilcox, *S & R 7586, S & R 7587.*

*A. oregonensis* (Nutt.) Cronquist. $2n = 9_{II}$. **California.** Del Norte Co.: US-199 W of Gasquet, *8519.* Siskiyou Co.: For. Serv. Hwy 93 NW of Salmon Forks, *8479.* Sierra Co.: CA-94 9.1 km E of Downieville P.O., *8411.* Yuba Co.: ca. 9000 La Porte Rd. (Co.Rd-E21) near Brownsville, *8413.* $2n = 18$. **California.** Calaveras Co.: CA-4 8.3 km W of Bear Valley Rd., *8781.* Eldorado Co.: S of Fallen Leaf Lake, Camp Richardson, *S & Ch 8911.*

*A. radulina* Gray. $2n = 27 = 3x$. **California.** San Mateo Co.: CA-35 27.4 km S of CA-92, *S & Ch 8914.*

*Aster* subg. *Aster* sect. *Dumosi* ($x = 8$)

*A. anomalus* Engelmann. $2n = 16$. **Oklahoma.** Leflore Co.: OK-1 E of Talimena, *8270.*

*A. borealis* (Torr. & Gray) Prov. $2n = 16$. **Saskatchewan.** 2.5 mi. W of Carragana, *Hooper & Baker 83073122.* $2n = 32$. **Minnesota.** Aitkin Co.: MN-18 SW of McGrath, 4.0 km E of MN-65, *S 9068.*

*A. bracteolatus* Nutt. $2n = 16$. **California.** Siskiyou Co.: Mt. Shasta City, *8459.*

*A. ciliolatus* × *A. lanceolatus.* $2n = 48$. **Saskatchewan.** NE of Somme, *Hooper & Baker 84082601.*

*A. cordifolius* L. $2n = 16$. **Delaware.** New Castle Co.: DEL-82 S of Yorklin, *S & R 7623.* $2n = 32$. **Maine.** Washington Co.: ME-9 SW of Calais, *S & Keir 4904.* **Pennsylvania.** Bedford Co.: PA-26 N of Tatesville, *S & R 7672.* Mckeene Co.: Custer City, *S & R 7580.*

*A. dumosus* L. $2n = 16$. **Kentucky.** Allen Co.: US-231, 11.5 km W of US-31, *S & Ch 9108.* **South Carolina.** Chesterfield Co.: SC-109 5.9 mi. N of SC-145 N of Mckennon, *S & Ch 6078.* $2n = 32$. **Florida.** Okeechobee Co.: Fl-70 2 mi. E of Okeechobee, *S et al. 7511.*

*A. laevis* L. var. *guadalupensis* A. G. Jones. $2n = 24_{II}$. **Texas.** Culberson Co.: Guadalupe Mountain National Park, Bowl Trail, *8179.* $2n = 48$. **Texas.** Culberson Co.: Guadalupe Mountain National Park, *8183.*

*A. laevis* L. var. *laevis.* $2n = 48$. **Michigan.** Crawford Co.: US-27 2 mi. S of Otsego Co., *S & Ch 4978.* Delta Co.: US-421 4.7 km E of Bank R., *S & Ch 5022.*

Table 1. Continued.

Mackinac Co.: Pt. aux Chenes, *S & Ch 5001*. Roscommon Co.: US-27 5 mi. S of Crawford Co., *S & Ch 4977*. **Minnesota.** Lincoln Co.: US-75 S of Lake Benton, *S & Ch 5132*. **Missouri.** Harrison Co.: US-136 W of Bethany, *S & Ch 5233*. **Pennsylvania.** Centre Co.: PA-144 W of Pleasant Gap, Nittany Mts., *S & R 7600*. **Wisconsin.** Douglas Co.: WI-27 2.1 km N of Co.Rd-2A, WNW of Barnes, *S 9081*.

*A. lanceolatus* Willd. ssp. *hesperius* (Gray) Semple & Chmielewski. $2n = 64$. **North Dakota.** Barnes Co.: Valley City, *S & Bt 6956*.

*A. lanceolatus* ssp. *lanceolatus*. $2n = 64$. **New York.** Cortland Co.: NY-281 2 mi. NE of Preble, *S 6799*. Onondago Co.: junction of US-20 and I-81, *S 6798*.

*A. lanceolatus* spp. *lancelatus* × *A. pilosus*. $2n = 48$. **Ontario.** Bruce Co.: 18.2 km S of Gilles Hill, *Ch 2028*.

*A. lateriflorus* L. var. *lateriflorus*. $2n = 16$. **Minnesota.** Mille Lacs Co.: US-169 between Rum River Rest Area and road to Onamia, *S 9065*.

*A. lateriflorus* L. var. *tenuipes* Wieg. $2n = 16$. **Ontario.** Renfrew Co.: NW of Deep River, along Ottawa R. 300 m NW of Mcfarlanes Point, *Brunton & McIntosh 7536*.

*A. lentus* Greene. $2n = 32_{II}$. **California.** Napa Co. Napa City, corner of Big Ranch Rd. and Trancas St., *8579*.

*A. lowrieanus* Porter. $2n = 16$. **Tennessee.** Cocke Co.: Co.Rd NW of Hartford, *S, Brammall & Hart 3015*.

*A. occidentalis* Nutt. $2n = 16$. **California.** Mono Co.: E of Tioga Pass, Aspen Grove Campground, *8715*; CA-108 W of West Walker R., *8721*. Plumas Co.: SW of Crescent Mills, *S et al. 5717a*. $2n = 32$. **California.** Mono Co.: Tioga Pass 0.25 mi. E of Yosemite National Park, *8690*. Siskiyou Co.: SE of Etna, CA-3 at rd. to Gazelle, *8499*. **Idaho.** Custer Co.: W of Sunbeam, *S & Bt 7051*. **Oregon.** Lane Co.: Willamette N.F., OR-242, 11.9 mi. E of OR-126, *S & Bt 7166*. $2n = 40$. **California.** Plumas Co.: SW of Crescent Mills, *S et al. 5717b*.

*A. ontarionis* Wiegand. $2n = 32$. **Ontario.** Brant Co.: Paris, *Ch 1431*. **Kentucky.** Warren Co.: US-213 10.9 mi. SE of I-65 (Bowling Green), *S & Ch 9104*.

*A. pilosus* Willd. var. *pilosus*. $2n = 32$. **Ontario.** Lambton Co.: Bosanquet Twp, Ipperwash Rd., *Ch 2239*; entrance to Ipperwash Provincial Park, *Ch 2240*. **Tennessee.** Rutherford Co.: E of Silver Hill on Al Sup Mill Rd., *S & Ch 9113*.

*A. pilosus* Willd. var. *pringlei* (Gray) Blake. $2n = 48$. **Ontario.** Halton Co.: S of Moffatt, *Ch 2374*. Niagara Reg. Mun.: N of Snyder, junction of Sommerville Rd. and Sodom Rd., *Ch 1754, 1755*. Manitoulin Dist.: Manitoulin Is., South Baymouth, ferry dock, *Ch & R 1271*. **Wisconsin.** Douglas Co.: margins of kettle hole pond by WI-27, WNW of Barnes, *S 9079*.

*A. prenanthoides* Torr. & Gray. $2n = 32$. **New York.** Cattaraugus Co.: W of Limestone, *S & R 7575*. **Virginia.** Nelson Co.: VA-56 W of Montebello, *S & Ch 5925*.

*A. priceae* Britt. $2n = 64$. **Tennessee.** Davidson Co.: La Vergne, TN-171 just N of US-41, *S & Ch 9125*; Rutherford Co.: US-70 E of Murfreesboro, 0.4 km W of Baxter Rd., *S & Ch 9126*; near Silver Hill, Al Sup Mill Rd., 0.6 km E of US-231, *S & Ch 9112*; US-231 ca. 5 km S of Vine, *S & Ch 9127*. Wilson Co.: US-231 N of Lebanon, *S & Ch 9128* (white rays), *9130* (blue rays).

Table 1. Continued.

*A. puniceus* L. $2n = 16$. **Virginia.** Nelson Co.: VA-56 W of Montebello, *S & Ch 5924.*

*A. shortii* Lindl. $2n = 16$. **Kentucky.** Allen Co.: US-231, just SW of Scottsville, *S & Ch 9106*. $2n = 32$. **Tennessee.** Wilson Co.: SE of Vine, Jennings Pond Rd., 0.5 km E of US-231, *S & Ch 9115.*

*A. undulatus* L. $2n = 32$. **Maryland.** Washington Co.: US-40 N of Greenbrier State Park, *S & R 7661.* **Virginia.** Albemarle Co.: US-29 N of Coveville, *S & Ch 5933.* Northumberland Co.: VA-200 3.6 mi. S of Burgess, *S & Ch 5986.*

*Aster* other subgenera ($x = 9$)

*A.* (*Oreastemma*) *alpigenus* (Torr. & Gray) Gray. $2n = 18$. **California.** Siskiyou Co.: Mt. Shasta, meadow by A-10, *8450*. $2n = 36$. Mono Co.: Tioga Pass, 0.25 mi. E of Yosemite National Park, *8688.*

*A.* (*Eucephalus*) *glaucodes* Torr. & Gray. $2n = 18$. **Utah.** Garfield Co.: UT-12, NE of Tropic, *S & Ch 8902*. San Pete Co.: W of Ephraim, *S & Ch 8890.* Utah Co.: UT-220 13.1 km E of UT-92 E of American Fork, *S & Ch 8880.* Wasatch Co.: UT-220 15 km E of UT-92 E of American Fork, *S & Ch 8879.* **Wyoming.** Albany Co.: US-130 8.5 km W of Centennial, *S & Ch 8862.*

*A.* (*Doellingeria*) *reticulatus* Pursh. $2n = 9_{II}$. **Florida.** Leon Co.: S of Bloxham, Forest Rd-320 2.2 km W of Forest Rd-344, *S & Ch 9176*; SE of Bloxham, junction of Forest Rds-344 and 304, *S & Ch 9177.* **Georgia.** Colquitt Co.: GA-33 NE of Moultrie, *S & Ch 9171.*

*A.* (*Eucephalus*) *wasatchensis* (M. E. Jones) Blake. $2n = 18$. **Utah.** Iron Co.: UT-14 26.2 km SE of Cedar City, *S & Ch 8904.*

*Aster* subg. *Oxytripolium* ($x = 5$)

*A. subulatus* Michx. var. *ligulatus* Shinners. $2n = 5_{II}$. **Oklahoma.** Atoka Co.: OK-7 just W of Muddy Boggy Creek, W of Farris, *8261.* **Texas.** Stonewall Co.: US-83 N of Aspermont, *8229.*

*A. tenuifolius* L. var. *tenuifolius.* $2n = 10$. **Maryland.** Queen Annes Co.: US-301 1 km E of drawbridge N of Gasonville, *S & R 7632.*

*Benitoa occidentalis* (Hall) Keck. $2n = 5_{II}$. **California.** Fresno Co.: CA-198 (NW of MP 9.0) SW of Colwell Rd., *S & Ch 8945.*

*Corethrogyne californica* DC. var. *obovata* (Benth.) O. Ktze. $2n = 5_{II}$. **California.** Mendocino Co.: CA-1 S of Westport, N of Mackerricher State Park, *8536.*

*C. filaginifolia* (Hook. & Arn.) Nutt. var. *brevicula* (Greene) Canby. $2n = 5_{II}$. Kern Co.: W of Freeman Junction, CA-178 ca. 17 km W of Onyx, *8650*. $2n = 10$. **California.** Kern Co.: W of Lake Isabella, Kern R. Recreation Area, below main dam, *S & Ch 8951.*

*C. filaginifolia* (H. & A.) Nutt. var. *peirsonii* Canby. $2n = 5_{II}$. **California.** Kern Co.: S of Tehachapi, Water Canyon Rd., *S & Ch 8958.*

*C. filaginifolia* (Hook. & Arn.) Nutt. var. *sessilis* (Greene) Canby. $2n = 10$. **California.** San Bernardino Co.: CA-18 2 km E of Santa's Village, *S & Ch 8977.*

*C. filaginifolia* (H. & A.) Nutt. var. *virgata* (Benth.) Gray. $2n = 5_{II}$. **California.** Monterey Co.: G-18 W of Greenfield, *8608.* San Luis Obispo Co.: Morro Bay, beach dunes N of The Rock, *8618.*

*C. leucophylla* Jepson. $2n = 5_{II}$. **California.** S of Big Sur, Pfeiffer Beach, *S & Ch 8929.*

Table 1. Continued.

*Chrysopsis mariana* (L.) Ell. $2n = 4_{II}$. **Florida.** Leon Co.: SW of Bloxham, Forest Rd-320 just E of FL-375, *S & Ch 9175.*

*Croptilon divaricatum* (Nutt.) Raf. var. *divaricatum.* $2n = 4_{II}$. **North Carolina.** Harnett Co.: NC-27 1.4 km SW of Lillington, *Canne 616.*

*Croptilon divaricatum* var. *hookerianum* (Torr. & Gray) Shinners. $2n = 12$. **Texas.** Lee Co.: US-77 4.3 mi. N of Giddings (US-290), *S & Bt 3363.*

*Eastwoodia elegans* Brandegee. $2n = 9_{II}$. **California.** San Joaquin Co.: 17.8 mi. E of Livermore on Co.Rd-J2, *L 3056.*

*Ericameria arborescens* (Gray) Greene ssp. *arborescens.* $2n = 9_{II}$. **California.** Santa Clara Co.: CA-130 5.1 km E of Mt. Hamilton, *8589.*

*E. cuneata* (Gray) McClat. $2n = 9_{II}$. **California.** Inyo Co.: W of Lone Pine, Whitney Portal Rd., *8667.* Kern Co.: E of Democrat Springs, between CA-178 and Kern R. 31.2 km SW of CA-155, *S & Ch 8956.* Tuolumne Co.: Pigeon Flat Campground, by Middle Fork of Stanislaus R., E of Dardanelle, *8732.*

*E. ericoides* (Less.) Jepson. $2n = 9_{II}$. **California.** S of Big Sur, Pfeiffer Beach, *S & Ch 8928.*

*E. laricifolia* (Gray) Shinners. $2n = 9_{II}$. **New Mexico.** Luna Co.: S of Dening, near entrance to Spring Canyon State Park, *S & Ch 9038.*

*E. pinifolia* (Gray) Hall. $2n = 18$. **California.** Los Angeles Co.: Claremont, Mt. Baldy Rd. NE of Padua Ave., *S & Ch 8972.*

*Erigeron breweri* Gray. $2n = 9_{II}$. **California.** Alpine Co.: CA-4 3.5 km E of Lake Alpine, W of Pacific Grade Summit, *8776.*

*E. glaucus* Ker. $2n = 9_{II}$. **California.** Mendocino Co.: CA-1 S of Rockport, *8532.* Sonoma Co.: CA-1 10.1 km S of county line, Pebble Beach Coastal Access, *8545*; CA-1 6 km N of Bodega Bay, just N of Schoolhouse Beach, *8577.*

*E. nematophyllus* Rydb. $2n = 9_{II}$. **Wyoming.** Albany Co.: Medicine Bow Nat'l For. 2.5 km by rd. SE of junction of I-80 and Happy Jack Rd., *S 8799.*

*E. simplex* Greene. $2n = 9_{II}$. **Colorado.** Lake Co.: CO-91 N of Climax below pass, *S 8801.*

*E. strigosus* Muhl. $2n =$ ca. $9_{II}$. **Tennessee.** Morgan Co.: TN-52 ca. 0.5 mi. W of Rugby, *S, Brammall & Hart 3002.*

*Euthamia graminifolia* (L.) Nutt. $2n = 18$. **New York.** Ulster Co.: NY-52 E of Woodburne, *S, Ch & R 6502.* **Ontario.** Kenora Dist.: junct. Hwy-17 and Mameigwess Rd., *S et al. 6738.* **Vermont.** Addison Co.: VT-125 E of Middlebury, *S 6901.* **Virginia.** Culpepper Co.: VA-3 1.3 mi. NW of Lignum Vitae, *S & Ch 5947.*

*E. microcephala* Greene. $2n = 18$. **North Carolina.** Wilson Co.: US-117 3.4 mi. N of Wayne Co., S of Wilson, *S & Ch 6012.*

*E. occidentalis* Nutt. $2n = 9_{II}$. **California.** Mendocino Co.: US-101, Willits, *8554.* San Diego Co.: CA-76 5.7 km NW of CA-79 (Lake Henshaw area), *S & Ch 8988.* $2n = 18$. **California.** Inyo Co.: US-395 N of Lone Pine, S of aqueduct, *8670.* Mono Co.: Topaz, *S & Ch 8907.* San Luis Obispo Co.: Atascadero *8612.* San Mateo Co.: CA-1 7.5 km N of Santa Cruz Co.: 8596. Sierra Co.: CA-49, Fiddler Creek Campground W of Downieville, *8412.* Siskiyou Co.: CA-96 1.6 km W of Horse Creek, *8468.*

Table 1. Continued.

*Grindelia inuloides* Willd. $2n = 6_{II}$. MEXICO. **Mexico.** Just W of junction of MEX-136 and MEX-85(libre), *L 2396.*

*G. oxylepis* Greene. $2n = 6_{II}$. MEXICO. **Aguascalientes.** 11.8 mi. W of Ciudad Aguascalientes, *L 2689.* **Jalisco.** MEX-80 9.9 mi. E of Agua el Obispo, *L 2594.*

*G. stricta* DC. $2n = 12_{II}$. **California.** Mendocino Co.: CA-1 vicinity of Westport Union State Beach, *8534.*

*G. subdecurrens* DC. $2n = 6_{II}$. MEXICO. **Hidalgo.** Estacion Cazadero, *L 2546.*

*Gutierrezia californica* (DC.) Torr. & Gray. $2n = 8_{II}$. **California.** Alameda Co.: Corral Hollow Rd. 7.7 mi. W of I-15, *L 2962.* Fresno Co.: CA-198 5.6 mi. SW of CA-33, *L 3055.* Kern Co.: CA-33 9.6 mi. N of CA-46, *L 3033.* San Benito Co.: Clear Creek Rd., 1.8 mi. N of southern end, *L 3036*; 12.6 mi. N of southern end, *L 3037.* Santa Barbara Co.: CA-33 4.1 mi. N of county line, *L 3031.* Stanislaus Co.: Corral Hollow Rd., 3.5 mi. W of I-580, *L 3059.* Yolo/Colusa Cos.: CA-16 0.7 mi. NW of Cache Creek Regional Park (middle site), *L 3043.* $2n = 12_{II}$. **California.** Alameda Co.: East Bay Regional Park, Dunn Trail Loop N of Admin. Bldgs., *L 2959.* Kern Co.: CA-33 2.6 mi. N of Maricopa, *L 3032.* Marin Co.: Angel Island State Park, above Camp Reynolds, *L 3040.* Riverside Co.: CA-74 28.1 mi. E of Kern Camp Summit, *L 3028.* Stanislaus Co.: Arroyo del Seco 6.6 mi. W of Patterson, *L 2961.* Ventura Co.: CA-33 11.4 mi. N of southern boundary of Los Padres Nat'l Forest, *L 3029.*

*G. sarothrae* (Pursh) Britt. & Rusby. $2n = 4_{II}$. **California.** San Diego Co.: CA-76 0.2 km W of CA-79, *S & Ch 8987.* CA-67 at Posthill Rd. N of Lakeside, *L 3022.* Willows Rd. at I-8, *L 3021.* **Colorado.** Boulder Co.: Boulder, N Gleenwood St. on 30th St., *L s.n.* Moffat Co.: Dinosaur Nat'l Monument, Yampa R. at Deerlodge Campground, *L 2934.* Montrose Co.: Rd-90 (from Naturita to Oak Grove) 2 mi. NE of San Miguel R., *L 2943.* **Idaho.** Bannock Co.: I-15 7 mi. S of Inkom, *L 3049.* **Nevada.** Clark Co.: Christmas Tree Pass Rd. 10.3 mi. E of US-95, *L 3009*; 9.1 mi. E of US-95, *L 3007.* NV-157 2.2 mi. E of US-95, *L 3001.* **Oregon.** Malheur Co.: US-95 22.5 km E of Rome, at Rock Crossing Creek, *L 3051.* US-95 6.5 mi. N of southern end of Succor Creek Recreation Area road, *L 3050.* Morrow Co.: OR-74 2.6 km E of Ione, *L 3054*; 20.1 km S I-84, *L 3055.* **Utah.** Millard Co.: T24S R4 1/2W S9, *L 3047, L 3048.* Uinta Co.: US-40 at mile post 173, *L 2936.* $2n = 8_{II}$. **Arizona.** Maricopa Co.: Vulture Mine Rd. 1.2 mi. S of US-60, *L 2804.* **California.** Riverside Co.: CA-74 21.6 mi. E of Kern Camp Summit, *L 3027.* San Diego Co.: Crestwood Rd. 2.4 mi. S of I-8, *L 3018.* CA-78 6.6 km E of Ramona, *L 3028.* **Oregon.** Gilliam Co.: I-84 11.2 km E of Rufus exit, *L 3052.* $2n = 12_{II}, 16_{II}$ (irregular meiosis). **Utah.** Dinosaur Nat'l Monument, Split Mountain Campground, *L 2938.*

*G. solbrigii* Cabreara. $2n = 20_{II}$. ARGENTINA. **Chubut Prov.**: Pto. Piramides, *H. Cordo s.n.*

*G. sphaerocephala* Gray. $2n = 4_{II}$. **Texas.** Brewster Co.: Alpine, Sul Ross State University campus, *L 2972.* Hudspeth Co.: US-62 W of Salt Flat, just E of FR-1437, *8159.* $2n = 4_{II} + 0 - 1_{supernumerary}$. **Texas.** Pecos Co.: US-67 2 mi. SW of I-10, *L 2969.*

Table 1. Continued.

*Gymnosperma glutinosum* (Spreng.) Less. $2n = 8_{II}$. **Texas.** Brewster: 19 mi. N of Alpine, *L 2971*. Jeff Davis Co.: TX-17 13 mi N of Fort Davis, *L 2974*.

*Haplopappus gracilis* (Nutt.) Nutt. $2n = 2_{II}$. **Arizona.** Cochise Co.: Portal Rd. W of Portal, 1 km W of Research Station of the Amer. Museum Natural Hist., *7993*. **New Mexico.** Luna Co.: S of Denning, near entrance to Spring Canyon State Park, *S & Ch 9037*.

*H. havardii* Waterfall. $2n = 4_{II}$. **Texas.** Hudspeth Co.: US-62 W of Salt Flat, just E of FR-1437, *8156*.

*H. spinulosus* (Pursh) DC. $2n = 4_{II}$. **Texas.** Culberson Co.: TX-54 12 km N of Van Horn, *8188*.

*H. spinulosus* ssp. *australis* (Greene) Hall. $2n = 4_{II}$. **Texas.** Hartley Co.: US-87 8 mi. SE of Dalhart, *S & Shea 1458*.

*H. spinulosus* ssp. *spinulosus*. $2n = 4_{II}$. **North Dakota.** Sargent Co.: ND-11 1.2 km E of Genesco, *S & Brammall 2686*. **Saskatchewan.** Trans Canada Hwy-1, just E of Balgonie, *S & Shea 1919*; Moose Jaw, 1 mi. W of SASK-2, *S & Shea 1932*; 2 mi. W of Waldeck, *S & Shea 1939*.

*H. squarrosus* Hook. & Arn. $2n = 5_{II}$. **California.** Monterey Co.: S of Big Sur, Pfeiffer Beach, *S & Ch 8930*.

*H. squarrosus* Hook. & Arn. ssp. *squarrosus*. $2n = 5_{II}$. **California.** San Luis Obispo Co.: CA-41 just E of Morro Bay, *8616*.

*H. squarrosus* Hook. & Arn. ssp. *grindelioides* (DC.) Keck. $2n = 5_{II}$. **California.** Santa Barbara Co.: bluffs along US-101 between Gaviota and Refugio State Beach, *8625*. Ventura Co.: CA-150 W of Ojai, *8627*.

*Heterotheca grandiflora* Nutt. $2n = 9_{II}$. **California.** Tulare Co.: W of Three Rivers, *S et al. 5643*.

*H. jonesii* (Blake) Welsh & Atwood. $2n = 9_{II}$. **Utah.** Kane Co.: UT-90 ca. 15 mi. W of Mt. Carmel Jct., *S 8829*.

*H. rutteri* (Rothr. in Gray) Shinners. $2n = 18$. **Arizona.** Santa Cruz Co.: SW of Sonoita, AZ-82 5 km SW of AZ-83, *S & Ch 9030*.

*H. zionensis* Semple. $2n = 9_{II}$. **Utah.** Kane Co.: UT-9 1 km E of Zion Nat'l Park, *7877*.

*Isocoma veneta* (H.B.K.) Greene. $2n = 6_{II}$. **California.** San Luis Obispo Co.: CA-41 just E of Morro Bay, *8617*. Santa Barbara Co.: bluff along US-101 between Gaviota and Refugio State Beach, *8626*.

*Lessingia nemaclada* Greene. $2n = 5_{II}$. **California.** Kern Co.: CA-155 13.9 km E of Glenville, *S & Ch 8948*. Siskiyou Co.: CA-3 SE of Etna, *8497*; CA-96 1.6 km W of Horse Creek, *8467*.

*Machaeranthera canescens* (Pursh) Gray. $2n = 8$. **Oregon.** Deschutes Co.: US-20 3.6 mi. NW of Sisters, *S & Shea 1984*.

*M. grindelioides* (Nutt.) Shinners. $2n = 8_{II}$. **Utah.** Garfield Co.: UT-12 S of Boulder, *S 8824*.

*Macronema greenei* (Gray) Greene. $2n = 9_{II}$. **California.** Glenn Co.: For. Hwy-7 near Mendocino Pass, Plaskett Meadows Recreation Area, *8556*.

*M. suffruticosa* Nutt. $2n = 9_{II}$. **Nevada.** Washoe Co.: NV-431 at Ophir Creek Trailhead, *8366*.

Table 1. Continued.

*Pyrrocoma racemosa* (Nutt.) T. & G. var. *sessiliflora* (Greene) Mayes. $2n = 6_{II}$. **California.** Inyo Co.: US-395 just S of L.A. Aqueduct, N of Lone Pine, *8669*.

*Solidago altissima* L. var. *altissima*. $2n = 27_{II}$. **Illinois.** Bureau Co.: W of Princeton, I-80 9.0 km E of IL-88, *7689*.

*S. caesia* × *rugosa*. $2n = 18$. **Maryland.** Washington Co.: US-40 N of Greenbrier State Park, *S & R 7657*.

*S. californica* Nutt. $2n = 18$. **California.** Kern Co.: CA-178 between Onyx and Weldon, *8651*. Riverside Co.: CA-243, Fuller Creek, Lake Fulmore Recreation Area, *S & Ch 8980*. Siskiyou Co.: SE of Etna, CA-3 at rd. to Gazelle, *8498*. CA-96 11 km E of town of Klamath River, *8465*. Sonoma Co.: CA-1 between Valley Ford and Bodega Bay, *8578*. Tuolumne Co.: CA-108 E of Dardanelle (3.7 km E of Kennedy Meadow Rd.), *8730*.

*S. canadensis* L. $2n = 18$. **California.** Alpine Co. CA-4 E of Pacific Grade Summit E of Bear Valley, *8786*. Butte Co.: between Inship and Butte Meadows at For. Rd. 150b, *8430*; SW of Butte Meadow along Butte Creek, *8431*; Jonesville, *8432*. Calaveras Co.: Poison Spring, W of Bear Valley, *8782*. Mendocino Co.: CA-1 1 km N of Pt. Arena, *8543*; CA-1 4.5 km S of city limit of Pt. Arena, *8550*. Mono Co.: CA-108 0.5 km W of Marine Corps Mountain Warfare Training Center, *8725*. Plumas Co.: Little Grassy Lake Rd. between La Porte and Quincy, *8416*. San Mateo Co.: CA-1 ca. 1 km S of Pescadero State Beach, *8591*. Siskiyou Co.: Etna Summit, SW of Etna on For. Hwy.-93, *8494*; Mt. Shasta City, East Lake St., *8460*. Tulare Co.: T-41 5.0 km W of Sherman Pass Summit E of Johnsondale, *8660*. **Oregon.** Douglas Co.: OR-230 9.7 mi. N of OR-62, *S & Bt 7151B*. $2n = 18_{II}$. **California.** Mendocino Co.: CA-1 10 km N of Cleome, N of MacKerricher State Park, *8537*. $2n = 36$. **California.** Mono Co.: CA-89 4.5 km N of Nevada Co. line, *8403*. **Montana.** Broadwater Co.: US-287 21 mi. E of Townsend, *S & Bt 7007*. $2n = 54$. **Utah.** Juab Co.: Mt. Nebo Scenic Rd., Ponderosa Campground, *S & Ch 8889*.

*S. canadensis* L. var. *canadensis*. $2n = 18$. **Illinois.** Fulton Co.: US-136 W of Illinois R., *S & Bt 7379*.

*S. confinis* Gray. $2n = 9_{II}$. **California.** Ventura Co.: Fillmore, Squaw Flat Rd. at N end of A St., *S & Ch 8970*. $2n = 18$. **California.** Riverside Co.: Lake Hemet region, CA-74 6.5 km S of CA-243, *S & Ch 8984*.

*S. flexicaulis* L. $2n = 36$. **Minnesota.** Mille Lacs Co.: N of Milaca, rest area on US-169, *S 9063*. **Wisconsin.** St. Croix Co.: E of Clifton Spring Golf Course, near Dept. Recreation Boat Access, *S et al. 8856*. Sheboygan Co.: Kettle Moraine State Forest, S of Greenbush Picnic Area, *S 9090*.

*S. gigantea* Ait. $2n = 18$. **Tennessee.** Marshall Co.: Henry Horton State Park, Wilhoile Mill Hiking Trail, *S & Ch 9118*.

*S. glutinosa* Nutt. ssp. *glutinosa* var. *glutinosa*. $2n = 18$. **Alaska.** Alaska Hwy (MP1368), NW of Tok, 12 km NW of Dot Lake, just past Berry Bridge, *CC2456*. **Yukon Territory.** Klondike Loop, 12 km S of Pelly Crossing near the 2nd lake, *CC2665*.

*S. juncea* Ait. $2n = 18$. **Pennsylvania.** Centre Co.: PA-144 2 km S of Potters Mill, *S & R 7604*.

*S. lepida* DC. $2n = 18$. **California.** Eldorado Co.: CA-89 6 mi. W of Woodford, *S & Ch 8910*. Sierra Co.: CA-49 W of Yuba Pass, *8406*.

Table 1. Continued.

*S.* aff. *lepida* DC. $2n = 36$. **British Columbia.** Hwy-24 50 km E of Lone Butte, *CC-BC1.*

*S. missouriensis* Nutt. $2n = 18$. **Wyoming.** Albany Co.: US-130 8.5 km W of Centennial, *S & Ch 8861.*

*S. multiradiata* Ait. $2n = 18$. **California.** Mono Co.: Lake Mary Rd. ca. 3 km E of Horseshoe L., W of Mammoth Lakes, *8678*; Tioga Pass, just E of Yosemite Park, *8693.* **Utah.** Garfield Co.: ca. 0.5 km W of Hell's Backbone Bridge, N of Escalante, *S & Ch 8901.* San Pete Co.: For. Rd. along crest of Wasatch Plateau, S of For. Rd. to US-89 (E of Manti), *S & Ch 8893.* $2n = 36$. **Alaska.** Steese Hwy, 2 km NE of Captain Creek, 8 km NE of Aurora Borealis Research Station, *CC2396.* **British Columbia.** Haines Hwy 1 km N of Stanley Creek, Chilkat Pass, *CC2524.* **Northwest Territories.** Happy Valley Campground, *CC2634.*

*S. nana* Gray. $2n = 18$. **Utah.** Dagget Co.: US-191 18.2 km S of Dutch John, *S & Ch 8872.*

*S. parryi* (Gray) Greene. $2n = 18$. **Wyoming.** Albany Co.: US-130, Snowy Mt. Range, Libby Flats, *S & Ch 8866.*

*S. rigida* L. ssp. *humilis* (Porter) Heard & Semple. $2n = 9_{II}$. **Wisconsin.** Adams Co.: WI-82, E of Co.Rd-B, *S et al. 8843.* $2n = 18$. **Wisconsin.** Jackson Co.: US-10 8.5 mi. E of Osseo, *S & Ch 5070.*

*S. rigida* L. ssp. *rigida.* $2n = 18_{II}$. **Minnesota.** Hennepin Co.: Eden Prairie, Spring Rd. just W of county airport, *S et al. 8849.* $2n = 36$. **Wisconsin.** Winnebago Co.: junction of US-41 and WI-110, N of Oshkosh, *S 9088.*

*S. rugosa* Mill. $2n = 18$. **Illinois.** Jo Daviess Co.: Tapley Woods Forest Res., US-20, *S 9051.* **Maryland.** Cecil Co.: US-1 NE of Rising Sun, *S & R 7617.* **Ontario.** Halton Reg. Mun.: 2.3 km E of Campbellville, *Ch 2233.* Wellington Co.: Belwood Conservation Area, *Ch 2004.* Wentworth Reg. Mun.: Valens Swamp, *Ch 2235.* **Wisconsin.** Crawford Co.: US-61 SE of Soldiers Grove, *S 9052.* $2n = 36$. **Delaware.** New Castle Co.: S of Yorklin, DL-82 ca. 4 km W of DL-52, *S & R 7621.* **Pennsylvania.** Centre Co.: PA-144 W of Pleasant Gap, Nittany Mts., *S & R 7603.*

*S. sparsiflora* Gray. $2n = 9_{II}$. **Texas.** Culberson Co.: Guadalupe Mt., The Bowl, 7700′, *8182.* $2n = 18$. **Utah.** Utah Co.: American Fork Creek Canyon, 5 km E of UT-92, *S & Ch 8882.* $2n = 36$. **Utah.** Summit Co.: UT-150 12.7 km SE of Kamas, *S & Ch 8886.* Wasatch Co.: UT-220 (MP 22) W of Wasatch Mt. Park, W of Midway, *S & Ch 8876.*

*S. spathulata* DC. $2n = 9_{II}$. **California.** Mendocino Co.: CA-1 just N of rd. to Pt. Arena Lighthouse, *8542.* $2n = 18$. **California.** Mendocino Co.: CA-1, N of Anchor Bay, ca. 11 km N of Sonoma Co. line, *8548.*

*S. speciosa* Nutt. $2n = 18$. **Tennessee.** Marshall Co.: between Chapel Hill and Holtland, *S & Ch 9121.*

*S. spectabilis* (DC. Eaton) Gray. $2n = 18$. **California.** Mono Co.: shore of Mono Lake N of Lee Vining, *8717.*

*S. uliginosa* Nutt. $2n = 18$. **Wisconsin.** Bayfield Co.: WI-27 21.3 km S of Douglas Co.Rd-A (Barnes), *S 9083.* Douglas Co.: bog along US-2 E of Maple, *S 9072.*

*S. ulmifolia* L. $2n = 18$. **Illinois.** Adams Co.: Bluff Hall, rd. to church off IL-57,

Table 1. Continued.

*S & Bt 7366.* **Tennessee.** Marshall Co.: Henry Horton State Park, Wilhoite Mill Hiking Trail, *S & Ch 9119.*

*S. wrightii* Gray. $2n = 18$. **Arizona.** Yavapai, US-89 NE of Wilhoit, *S & Ch 8997.*

*Stephanodoria tomentella* (Robinson) Greene. $2n = 6_{II}$. MEXICO. **San Luis Potosi.** Las Tablas, *L 2920*; 0.4 mi. N of Las Tablas, *L 2535*; 0.7 mi. N of Las Tablas, *L 2913*; 300 yd W of Las Tablas, *L 2544.*

*Virgulaster ascendens* (Lindl.) Semple. $2n = 26$. **California.** Inyo Co.: vicinity of Glacier Lodge, *8673*. $2n =$ ca. $26_{II}$. **Utah.** Kane Co.: US-89alt. south edge of Kanab, *7882.*

*Virgulus* × *amethystinus* (Nutt.) Reveal & Keener. $2n = 10$. **Minnesota.** Pope Co.: Starbuck, *S & Ch 5095*. **Ontario.** North York, *Ch & Cameron 2335.*

*V. ericoides* (L.) Reveal & Keener. var. *ericoides*. $2n = 10$. **Minneosta.** Crow Wing Co.: MN-371, S of Brainerd, *8794*. Omstead Co.: US-14, SW of Rochester, *S 9053*. **Wisconsin.** Pierce Co.: Co.Rd-F, cliffs W side of Kinnickinnic R., *S et al. 8885.*

*V. ericoides* var. *pansus* (Blake) Reveal & Keener. $2n = 10$. **New Mexico.** NM-15 39.2 km N of US-180, N of Silver City, *S & Ch 9040.*

*V. falcatus* (Lindl.) Reveal & Keener. $2n = 10_{II}$. **Colorado.** Lincoln Co.: E of Arriba, I-70 2.6 km E of county line, *7712.*

*V. fendleri* (Gray) Reveal & Keener. $2n = 10$. **Kansas.** Ford Co.: US-50 0.5 mi. E of county line, *S & Bt 7302.*

*V. novae-angliae* (L.) Reveal & Keener. $2n = 10$. **Missouri.** Calaway Co.: US-54 1 mi. N of Auxvasse, *S & Ch 5310.*

*V. oblongifolius* (Nutt.) Reveal & Keener. $2n = 20$. **Minnesota.** Hennepin Co.: Eden Prairie, Spring Rd. just W of county airport, *S et al. 8846.*

*V. patens* (Ait.) Reveal & Keener var. *phlogifolius* (Muhl.) Reveal & Keener. $2n = 10_{II}$. **Tennessee.** Rutherford Co.: near Silver Hill, Al Sup Mill Rd. 0.6 km E of US-231, *S & Ch 9114*. $2n = 20$. **Kentucky.** Allen Co.: just N of TN border, *S & Ch 9111.*

*V. pratensis* (Raf.) Reveal & Keener. $2n = 10$. **Florida.** Gadsden Co.: Co.Rd-269 0.5 mi. S of r.r. (River Junction, Chattahoochee), *Godfrey 82636.*

*V. sericeus* (Vent.) Reveal & Keener. $2n = 10$. **Minnesota.** Hennepin Co.: Eden Prairie, Spring Rd. just W of county airport, *S et al. 8847*. Washington Co.: just N of Stillwater, *S et al. 8858*. **Wisconsin.** Adams Co.: WI-82 1 km E of WI-13, N of Plainville, *S 8842.*

## Aster (excluding Virgulaster and Virgulus)

Reports for the genus *Aster* sensu Semple and Brouillet (1980a, 1980b) are listed alphabetically within subgenera. A number of these deserve comment, but most are merely confirmations of previous reports. All reports in Table 1 and previously published reports for *Aster laevis* are $2n = 48$ regardless of variety. The first

reports for *A. reticulatus* are in line with all previous reports for members of subg. *Doellingeria* sect. *Triplopappus*.

Numerous chromosome number counts have been reported for members of *Aster* (subg. *Aster* sect. *Dumosi*) subsect. *Porteriani* and were discussed by Semple and Chmielewski (1985). Only the data on *A. priceae* ($2n = 64$, Table 1) represent significant new information; this is the first report of the octoploid level for subsect. *Porteriani* and the species. Semple and Chmielewski (1985) reported a count of $2n = 32$ under the name *A. pilosus* var. *priceae* determined from a plant collected in northeastern Alabama (*S & Ch 6305*). The voucher for the report was re-examined and compared with very typical collections of *A. priceae* from Tennessee as well as the type of the taxon; *6305* is now assigned to *A. pilosus* var. *pilosus*. Thus, we reject our earlier tetraploid report for *A. priceae* and acknowledge that unfamiliarity with the taxon at the time resulted in the misidentification of a rather glabrate, bluish-rayed individual of var. *pilosus*. The tetraploid plant collected in 1981 did not have the decumbent to ascending growth form nor the distinctive bluish-green leaf color typical of the many plants of *A. priceae* we observed in the field at a number of sites in the fall of 1987. The generally larger size of the floral parts of *A. priceae* compared to other species of the subsection can be attributed in part, if not fully, to the higher ploidy level. Ploidy level alone is not likely to be the cause of the other distinctive features of the species. A multivariate morphometric analysis of all taxa in subsect. *Porteriani* is being prepared for submission by J.C.S. and J.G.C. and will more fully explain our decision to accept species status for the octoploid members of the complex.

The count of $3x = 2n = 27$ for *Aster radulinus* from San Mateo Co., California is noteworthy for two reasons. First, reports of triploids in the genus are extremely rare. Second, this is the second report of a triploid in the species; the first triploid was a plant collected in Mendocino Co., California (Semple et al., 1983). Diploids have been reported from two locations in southern Oregon and two locations in southern Washington (Semple, 1985). A pattern is suggested, but the number of reports is still very low. We provisionally suggest that a triploid, apomictic race of the species exists in the Coastal Ranges of California, in the hope of stimulating assistance with additional research on the species.

The $x = 5$ counts for members of *Aster* subg. *Oxytripolium* are in agreement with all previous reports for *A. subulatus* and *A.*

*tenuifolius*. Semple and Brouillet (1980a) did not exclude the subgenus from *Aster* for nomenclatural reasons, and we have adopted the same policy here. Reasons for excluding the group from *Aster* are discussed below.

**Gutierrezia**

Counts for the taxa of *Gutierrezia* ($x = 4$) are in keeping with the well documented occurrence of polyploidy in the genus (*see* Lane, 1985). All the South American species are high polyploids, and *G. solbrigii* (a decaploid, reported here for the first time) is no exception. The populations of *G. sarothrae* at Dinosaur National Monument on the Colorado-Utah border included diploid, hexaploid, or octoploid individuals. Meiotic behavior was irregular, indicating that either the polyploids and diploids may not be completely isolated or that the polyploids are unstable. Although the polyploids have been recognized taxonomically (Welsh, 1981), it was deemed wisest to treat the polyploids as *G. sarothrae* (Lane, 1985), until the breeding relationships are understood. A very intensive study of the populations is warranted.

**Solidago**

Only a few counts for *Solidago* warrant comment. The three tetraploid reports for *S. flexicaulis* listed in Table 1 are from Minnesota and Wisconsin. Semple et al. (1984) and Chmielewski and Semple (1985) noted that on the basis of a limited sample, only tetraploids occurred in the western and southern portion of the range; this finding remains true. For *S. rugosa,* the cytogeographic pattern is altered from that discussed by Semple et al. (1984); the occurrence of diploids in Illinois and Wisconsin (Table 1) indicates that no simple east-west cytotype pattern exists in *S. rugosa*. In the *S. canadensis* complex, diploid and tetraploid counts for populations in California are reported. In most cases these plants are readily assignable to *S. canadensis* ssp. *elongata* (Nutt.) Keck, but the counts are only reported to species in Table 1 due to the uncertain status of infraspecific taxa in the species.

**Comments on $x = 6$ Genera and Haplopappus sensu lato**

In the first two papers in this series (Semple, 1985; Semple and Chmielewski, 1987) the $x = 6$ taxa included in *Haplopappus* by

Hall (1928) were reported under that generic name in sections *Isocoma, Prionopsis* and *Pyrrocoma.* In Table 1, reports for these $x = 6$ taxa are listed in the appropriate segregate genera following the ideas of M. Lane on phylogeny (Lane and Hartman, 1984, 1985; Lane et al., 1987) based on data indicating that all $x = 6$ taxa in *Haplopappus sensu lato* as well as *Grindelia, Olivaea,* and *Xanthocephalum sensu* Lane (1983) belong to a monophyletic group that does not include *Haplopappus* (*sensu* Table 1; $x = 5$ and derived lower numbers). That *Stephanodoria* also belongs in this group is confirmed here by the counts of $2n = 6_{II}$. Lane and Hartman (1984, 1985) hypothesized that the base number of the genus would be $x = 6$. We do not consider it acceptable to lump all of the taxa in these genera into a single holophyletic genus. Therefore, we have adopted an alternative, which is admittedly a "splitter's" approach to generic limits, at least for the present, pending the results of research now in progress by other laboratories (University of Texas and University of Kansas) on chloroplast DNA restriction fragment polymorphisms.

Reports for $x = 9$ taxa included in *Haplopappus sensu* Hall (1928) are listed in Table 1 under *Ericameria* and *Macronema.* The species in these two genera, and those in *Chrysothamnus,* form a natural alliance that cannot be separated into well-defined groups worthy of generic recognition, unless arbitrary character limits are adopted. We think that all taxa probably should be included under a single generic name, *Chrysothamnus,* once nomenclatural priorities have been sorted out fully in studies in progress. Since the appropriate combinations are not yet available, the chromosome number reports are given under the segregate generic names.

## Generic Limits and the Ancestral Base Number of the Astereae

Our acceptance of a number of segregate genera is based on opinions favoring an $x = 5$ ancestral chromosomal base number for the entire tribe Astereae. Recognition of *Virgulus* (ancestrally $x = 5$) separate from *Aster* (ancestrally $x = 9$) continues in this paper. This separation raises the philosophical problem of how to deal nomenclaturally with the species first described as *Aster ascendens* Lindl. ($x = 13$; $n = 13, 26$), which Allen (1985) demonstrated to be of allopolyploid origin. The putative parents were *A. occidentalis* Nutt. ($x = n = 8$) and *V. falcatus* (Lindl.) Reveal

& Keener ($x = n = 5$; treated as *A. falcatus* by Allen). The $x = 13$ base number is unique in the tribe, and for this reason its origin is a special phenomenon that ought not to be dismissed casually on the grounds that asters are notorious for hybridizing. Admittedly, *Virgulaster ascendens* (Lindl.) Semple, the name under which counts for the species are reported in Table 1, is very similar morphologically to its putative $x = 8$ parent. However, the species includes the $x = 5$ as well as the $x = 8$ genome and both are reflected in its morphology, which is to be expected in an allopolyploid. If *Virgulus* is viewed as a concept that has irretrievably floundered "on the rocks of allopolyploidy" (Cronquist, 1985), then *Virgulaster* must be submerged as well. If this case of allopolyploidy is recognized for its special nature, a high peak in cytological evolution within the tribal landscape, then its existence does not mean that *Virgulus* must be abandoned. Cytological data can be seminal in understanding phylogenetic relationships in the Astereae that subsequently have been supported by previously overlooked morphological data; for example, separation of *Heterotheca* sect. *Phyllotheca* form *Chrysopsis* (*sensu* Semple et al., 1980) and the recognition of the virguloid asters (regardless of rank) as a distinct phylad of asters (Jones, 1980a, 1980b; Semple and Brouillet, 1980a, 1980b). Nomenclature must reflect phylogeny, if it is to be useful in predicting degrees of similarity in unexplored data bases. *Virgulus* may not be convenient as a generic concept, but it does provide a label for a monophyletic assemblage whose phylogenetic relationships to other taxa, including other asters, are not really understood. There are no data that conclusively show that *Virgulus* is derived from *Aster* via dysploidy (the latter being paraphyletic), or that *Aster* is derived in part or fully from *Virgulus* via allopolyploidy, or that either is ancestral to the other (the least likely option on the basis of morphology). Also, it is not clear how the oxytripolioid asters fit into the phylogeny. Pragmatically, use of the name *Virgulus* ensures that an $x = 5$ species in the genus is not included in studies as representative of the ancestrally $x = 9$ *Aster* (*sensu* Semple and Brouillet, 1980a, 1980b). For the same reason, *A.* subg. *Oxytripolium* (ancestrally $x = 5$; discussed below) also should be treated as a separate genus, but it is not for nomenclatural reasons.

Choice of $x = 9$ taxa to be included in studies on the ancestral chromosomal base number of the tribe is important. The phy-

logenetic position of *Aster pauciflorus* Nutt. (synonym: *A. hydrophilus* Greene) is critical in the interpretation of the results of some studies concerned with the base number question (Stucky and Jackson, 1975; Stucky, 1978; Gottlieb, 1981). The assumption has been made that *A. pauciflorus* is representative of the $x = 9$ species of *Aster,* at least in terms of genomic evolution, and that it is not a recently derived allopolyploid. If the species falls in the latter category, it is a most inappropriate organism for testing hypotheses on the numbers of gene loci to be expected in the higher base number taxa of the tribe (Gottlieb, 1981). Phyllary shape and margin features, rhizome features and the preference for brackish wetland habitats suggest a relationship between *A. pauciflorus* and the $x = 5$ members of *Aster* subg. *Oxytripolium* (*A. subulatus* and *A. tenuifolius,* Table 1). Jones (1980a, 1980b) treated *A. pauciflorus* as a member of the subgenus on the basis of unspecified morphological similarities. If *A. pauciflorus* is closely related to the oxytripolioid asters, then it is an allopolyploid with the $x = 4$ portion of the genome possibly coming from *Machaeranthera* sect. *Psilactis.* The chromosome pairing reported by Stucky and Jackson (1975) may reflect such an origin in the same manner that chromosome pairing between $x = 5$ and $x = 9$ taxa in *Chrysopsis* demonstrated the allopolyploid nature of the higher base number species (Semple and Chinnappa, 1980a, 1980b). One difference in the two cases involves the size of the derived genome which was greatly reduced in the case of *Aster pauciflorus,* but not in *Chrysopsis gossypina* (Michx.) Ell. Relevant are the unpublished data of a preliminary examination of gene loci number in *Chrysopsis.* Gottlieb (pers. comm. to J.C.S.) found no evidence to support the polyploid status of *C. gossypina,* but the results were "consistent with the hypothesis that the different chromosome numbers reflect aneuploid changes." However, cytological studies (Semple and Chinnappa, 1980b) clearly demonstrated that the $x = 9$ base number was of alloploid origin. Thus, the electrophoretic data turned out to be unrevealing in the case of *Chrysopsis.* In the case of *A. pauciflorus,* we believe similar results have been cited as evidence supporting an $x = 9$ ancestral base number for the tribe. Until a study is done involving other $x = 9$ species of *Aster* which are not putative recently-derived allopolyploids, it seems most reasonable to accept that the ancestral base number question, $x = 5$ versus $x = 9$, has not been resolved satisfactorily by electrophoretic or chromosome pairing

data published to date. Minimally, the uncertain phylogenetic position of *A. pauciflorus* disqualifies it as the species on which to rest conclusions about the ancestral base number of the Astereae. Whether $x = 5$ or $x = 9$ is ancestral in the Astereae is very important in setting generic limits and constructing phylogenies. If $x = 9$ is ancestral as suggested by Raven et al. (1960), then all lower base number taxa must be derived a number of times from higher base number taxa. If $x = 5$ is ancestral as suggested by Turner et al. (1961), then the several $x = 9$ phylads must be polyploid, including *Aster sensu* Semple and Brouillet (1980a). At present, the more frequently used nomenclatural schemes recognize a few large genera, such as *Haplopappus* (*sensu* Hall, 1928). These nomenclatural systems were proposed before cytological data were available, and thus they do not reflect the implications of such data. Nomenclature should reflect all information available, for this reason we have adopted unconventional, narrow generic limits in this paper.

We conclude with a cautionary note about resolving phylogenetic and nomenclatural problems in the Astereae via restriction enzyme fragment polymorphism data. Any data base that only can reveal the maternal line in a phylad cannot be relied upon alone to sort out patterns of reticulate evolution, although knowing conclusively the identity of one parent of an allopolyploid phylad will be very informative. Just as electrophoretic data have not been as conclusive as we might wish, so too will DNA studies in some cases provide ambiguous results in the Astereae and elsewhere.

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# FLORISTIC DYNAMICS OF A SMALL ISLAND COMPLEX IN LAKE WINNIPESAUKEE, NEW HAMPSHIRE

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## ABSTRACT

Three Mile Island, New Hampshire (U.S.A.), located on the northwest arm of Lake Winnipesaukee in central New Hampshire, is approximately 17.4 ha in size. The flora of this island has been studied intermittently by various botanists and naturalists since 1900. Surveys and collections of the vascular plant flora were undertaken by the authors between 1978 and 1985. A single synthetic list of the island's vascular flora was produced, including plants listed by all previous observers. A total of 363 species is here reported, including *Cypripedium arietinum,* a rare species listed by the state of New Hampshire. General characteristics of plant taxa lost and gained reflect the land use patterns of Three Mile Island, a continuum of small changes occupying eight decades.

Key Words: Vascular plant flora, vegetation dynamics, *Cypripedium arietinum,* Three Mile Island, Lake Winnipesaukee, New Hampshire

## GEOLOGICAL AND HUMAN HISTORY

The flora of Three Mile Island, Lake Winnipesaukee, New Hampshire (U.S.A.) has been studied intermittently by various botanists and naturalists since the island was purchased by the Appalachian Mountain Club in 1900 (Lawrence, 1901; Kelsey, 1902, 1903; Pease, 1911; Wilde, 1921; Hartmann, 1941; Sackett and Maciejowski, 1977; Maciejowski et al., 1981). The most extensive compilation of vascular plant species on the island (Pease, 1911) included notations and collections made by A. S. Pease (August, 1903), J. H. Emerton (May, 1906), and R. A. Ware (July, 1906). The present study is a flora of the vascular plants occurring on Three Mile Island from 1978 to 1985 and a comparison of this flora with that noted by Kelsey (1902), Pease (1911), and Hartmann (1941), with observations on vegetational changes that have occurred on the island since the turn of the century.

Three Mile Island is located on the northwest arm of Lake Winnipesaukee in central New Hampshire (Figure 1); it is approximately 17.4 ha in size. The island is managed by the Appalachian Mountain Club as a family camp, open primarily during July and August. Two small islands known as Hawk's Nest and Blueberry Islands (Figure 1) are also affiliated with the camp.

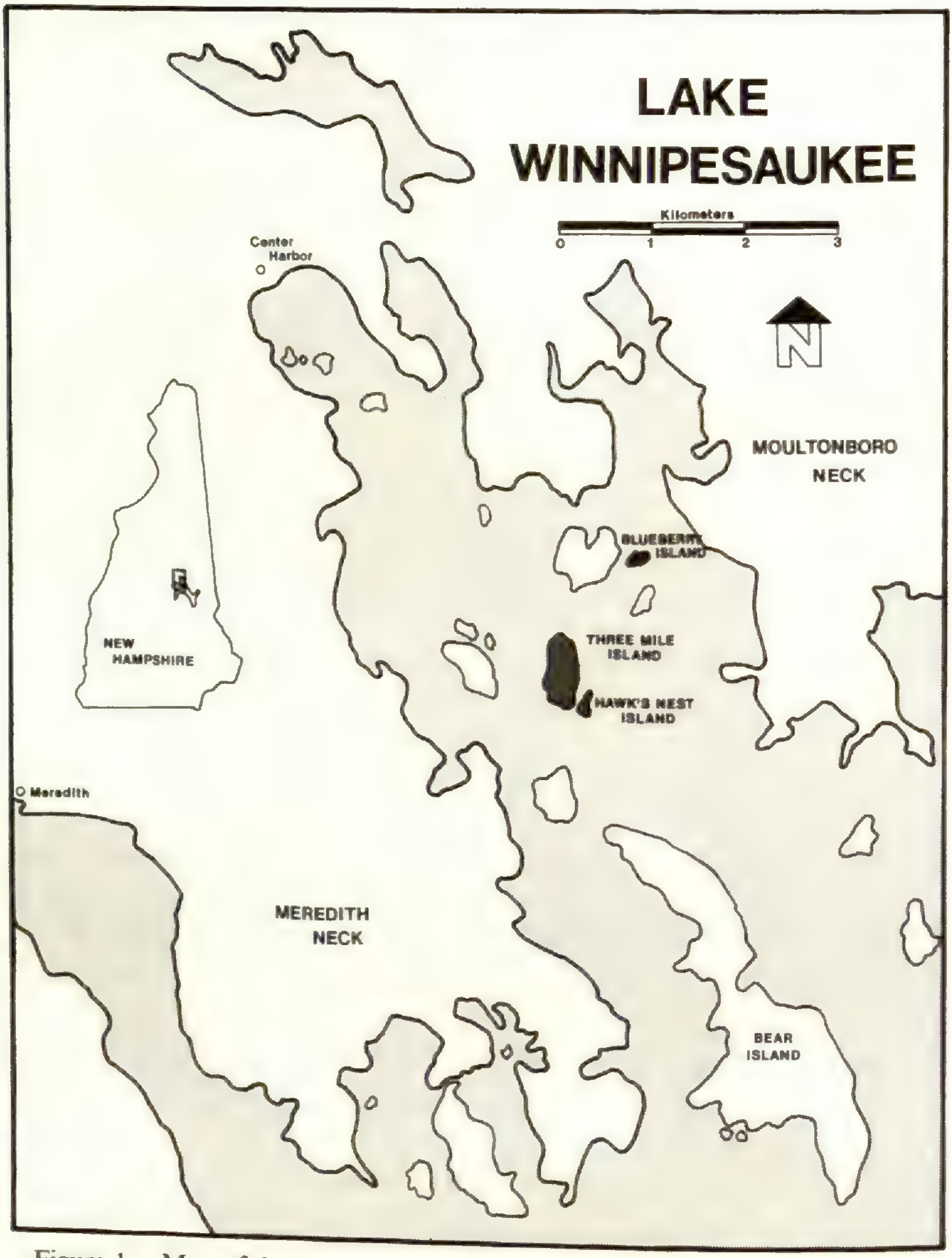


Figure 1. Map of the study area and location of the study sites (shown in gray shading) in New Hampshire, U.S.A.

The geology of the islands in Lake Winnipesaukee in the reach between Moultonboro Neck and Meredith Neck (Figure 1) is quite uniform. Bear, Pine, Black Cat, Three, Five, and Six Mile Islands are all comprised of outcrops of the Winnipesaukee Quartz Diorite, a medium-grained, gray quartz diorite (N.H. Highway Dept., 1940; Quinn, 1941). In places it is found in contact or in gradational sections with granite and diorite. The bedrock core of

Three Mile Island is covered with a surface mantle of broken blocks of bedrock from the local area produced by the intense frost-prying action which influenced this area immediately following the last glaciation. The mantle also contains unevenly distributed pockets of glacial till, comprised largely of silt, sand, and small stones. These pockets give way towards the island's shores to similar pockets of beach sand and washed lake-bottom deposits (pers. comm. from B. K. Fowler, 1975, to J. L. Trickey, member, Three Mile Island Camp Committee, in regard to geology of Three Mile Island). Maximum relief is only 16 m above mean lake level.

## VEGETATION

Records from the 1890's indicate the islands were then largely covered with a second-growth forest of poplars and birches, with an abundant evergreen understory of pines, hemlocks, and spruces (Rogovin, 1983). At the turn of the century the island's character was described as "picturesquely rocky," supporting a heavy stand of mixed timber with a richly diversified undergrowth of herbs and shrubs (Atkins, 1972). Today the island forests are dominated by *Fagus grandifolia, Quercus rubra,* and *Pinus strobus* (Maciejowski et al., 1981). Other prominent species include *Acer rubrum, Betula papyrifera,* and *Tsuga canadensis.* Present tree composition is characteristic of Braun's (1950) Hemlock–White Pine–Northern Hardwood forest. The understory is dominated by *Aralia nudicaulis* and *Gymnocarpium dryopteris*; the most prominent shrubs are *Vaccinium angustifolium* and *Gaylussacia baccata* (Maciejowski et al., 1981).

In 1903 an herbarium collection was started at Three Mile Island to document all vascular plants on the islands; since then, protection of the natural character of the island has been a continuing concern to both campers and management. Cutting for firewood is restricted to forest in the center of Three Mile Island, and coordination of activities on the islands adheres to a land use management plan (Sackett and Maciejowski, 1977; Maciejowski et al., 1981; Holland et al., 1983).

In May, 1901, H. P. Kelsey introduced 481 plants representing 60 predominantly woody species to Three Mile Island; of these, probably nine (Table 1) were indigenous (Pease, 1911). Kelsey (1902) also included in his list such southern and Alleghenian

Table 1. Total species reported, new taxa, and persistence from previous collections of plant species at Three Mile Island, New Hampshire, USA.

| | Number of Species | | | |
|---|---|---|---|---|
| Collector | Total Species Reported | New to TMI | Persistence of Non-Indigenous Species Introduced by Kelsey in 1901 | Persistence of Indigenous Species Reported by Pease (1911) |
| Kelsey (1902)* | 60 | — | — | — |
| Pease (1911) | 265 | — | 51 | — |
| Hartmann (1941)** | 193 | 31 | 9 | 153 |
| MMH/BAS (this study) | 243 | 66 | 10 | 157 |

* Nine species planted by Kelsey were indigenous to the islands.

** Ten species first observed on the islands by Hartmann persist today.

species as: *Liriodendron tulipifera, Magnolia acuminata, M. tripetala, M. fraseri, M. virginiana,* and *Halesia carolina* (*Mohrodendron carolinum* of Kelsey, 1902), all transplanted far to the north of their natural ranges.

E. G. Hartmann visited Three Mile Island during one week in early August, 1941 to note the changes that had occurred in the flora of the island in the thirty-year period since Pease's (1911) list was published. Hartmann (1941) was particularly interested "to see how many of the Allegheny Mountain plants were still to be found on the island." Although Hartmann did not undertake a thorough collection, 193 taxa of vascular plants were observed, and 31 of these species were not included in the 1911 list (Table 1). Of the indigenous plants listed by Pease, 67% were found, whereas only 28% of Kelsey's introduced species were seen. Hartmann (1941) suggested that there had been considerable mortality among the southern plants during their 40 years in a northern environment. Although Hartmann's notes are quite useful, there is no opportunity for a detailed comparison between her collection and ours since hers was not a comprehensive study, and no specimens are available from her 1941 visit.

## FLORA OF THREE MILE ISLAND

Surveys and collections of the vascular plant flora were undertaken by the authors between 1978 and 1985; collections were

made July 22–29, 1978; July 26–28, 1979; May 31–June 1, 1980; September 26–28, 1980; July 25–31, 1981; May 28–31, 1982; June 18–21, 1982; July 24–31, 1982; June 3–5, 1983; June 18–21, 1984; and August 17–18, 1985. Nomenclature follows Fernald (1950) for most of our collections; Tryon (1978) is our reference for the ferns. However, in an effort to produce a single synthetic list for the island, we have also included plants listed by Pease (1911) and by Hartmann (1941) even if we did not re-locate these species.

With the exception of the ferns, the name in the left column of our list is taken from Fernald (1950), the name [in brackets] is the name from Pease (1911), and the letters in the right column are symbols indicating sources of information (*see* Key below). Pease's (1911) nomenclature followed the 7th edition of Gray's Manual (Robinson and Fernald, 1908). Thus, the list below is a compilation of all plants noted on Three Mile Island during the twentieth century.

We were able to check many of our specimens against Pease's collection (now at NEBC) or against Ware's collection (partly at SCHN, partly at George Mason University, and partly at NEBC) or against Emerton's and anonymous collections (at George Mason University). The value of such early plant collections appropriately stored and maintained can never be over-estimated; in fact, a study such as this might well have ended with more questions than answers had not the original specimens been available for scrutiny. For example, the *Viburnum dentatum* L. recorded by R. Ware has now been split into *V. recognitum* Fern. for northern Arrow-wood and *V. dentatum* L. for southern Arrow-wood (Fernald, 1950); Ware's specimen confirmed that Three Mile Island supported the northern species in 1906.

KEY

A. Specimens of anonymous collectors with incomplete data (all pre-1911). In the A.M.C. herbarium (now at George Mason University).
E. Plants collected by J. H. Emerton in May, 1906. In the A.M.C. herbarium (now at George Mason University).
H. Plants noted (but not collected) by E. G. Hartmann in 1941.
K. Plants introduced by H. P. Kelsey in May, 1901.

M. Plants collected by M. M. Holland, 1978–85. At George Mason University herbarium.
P. Plants collected by A. S. Pease, August 24–25, 1903. In herbarium of A. S. Pease (now mostly at NEBC).
S. Plants recorded (but not collected) in B. A. Sorrie Field Notebook (1985).
T. Plants recorded (but not collected) in Three Mile Island Natural History Notebook (1964–85), but not including M. and S. above.
W. Plants collected by R. A. Ware, July 9–16, 1906. In A.M.C. herbarium (now at George Mason University).
# Plants included in a MS. list (but not necessarily collected) made by A. S. Pease in August, 1903.
–/–/– Not found before 1964.
* Not found since 1909.

## ANNOTATED CHECKLIST

EQUISETACEAE

*Equisetum pratense* Ehrh. –/–/– M.

LYCOPODIACEAE

*Lycopodium clavatum* L. W. M.
*L. complanatum* L. var. *flabelliforme* Fern. W. M.
*L. obscurum* L. W. M.

OPHIOGLOSSACEAE

*Botrychium dissectum* Spreng. [*B. obliquum* Muhl.] A. *
*B. simplex* E. Hitchc. –/–/– T.

OSMUNDACEAE

*Osmunda cinnamomea* L. W. M.
*O. claytoniana* L. H. M.
*O. regalis* L. # M.

POLYPODIACEAE

*Athyrium filix-femina* (L.) Roth [*Asplenium filix-femina* (L.) Bernh.] W. M.
*Dennstaedtia punctilobula* (Michx.) Moore [*Dicksonia punctilobula* (Michx.) Gray] W. M.
*Dryopteris clintoniana* (D. C. Eaton) Dowell [*Aspidium cristatum* (L.) Sw. var. *clintonianum* D. C. Eaton] P. *
*D. cristata* (L.) Gray var. *cristata* –/–/– M.

*D. intermedia* (Willd.) Gray [*Aspidium spinulosum* (O. F. Muell.) Sw. var. *intermedium* (Muhl.) D. C. Eaton] W. M.
*D. marginalis* (L.) Gray [*Aspidium marginale* (L.) Sw.] W. M.
*Gymnocarpium dryopteris* (L.) Newm. [*Phegopteris dryopteris* (L.) Fee] W. M.
*Onoclea sensibilis* L. A. M.
*Polypodium virginianum* L. [*P. vulgare* L.] W. M.
*Polystichum acrostichoides* (Michx.) Schott # M.
*Pteridium aquilinum* (L.) Kuhn var. *latiusculum* (Desv.) Underw. [*Pteris aquilina* L.] W. M.
*Thelypteris noveboracensis* (L.) Nieuwl. [*Dryopteris noveboracensis* (L.) Gray] H. M.
*T. palustris* Schott [*Aspidium thelypteris* (L.) Sw.] W. M.
*T. phegopteris* (L.) Slosson [*Phegopteris polypodioides* Fee] A. *
*Woodsia ilvensis* (L.) R. Br. recorded by "Miss Adams" in Pease (1911) *

TAXACEAE

*Taxus canadensis* Marsh. W. *

PINACEAE

*Abies balsamea* (L.) Mill. # *
*A. fraseri* (Pursh) Poir. K. *
*Chamaecyparis thyoides* (L.) BSP. K. M.
*Juniperus communis* L. var. *depressa* Pursh A. M.
*J. virginiana* L. K. *
*Larix laricina* (DuRoi) K. Koch H.
*Picea mariana* (Mill.) BSP. W. *
*P. pungens* Engelm. H.
*P. rubens* Sarg. –/–/– M.
*Pinus pungens* Lamb. K. H.
*P. resinosa* Ait. W. M.
*P. strobus* L. W. K. M.
*Tsuga canadensis* (L.) Carr. W. K. M.
*T. caroliniana* Engelm. K. *

SPARGANIACEAE

*Sparganium fluctuans* (Morong) Robins. H.

ZOSTERACEAE

*Potamogeton gramineus* L. [*P. heterophyllus* Schreb.] # *

*P. spirillus* Tuckerm. [*P. dimorphus* Raf.] P. *
*P. amplifolius* Tuckerm. –/–/– M. S.

ALISMATACEAE

*Sagittaria rigida* Pursh H.

GRAMINEAE

*Agropyron repens* (L.) Beauv. –/–/– M.
*A. trachycaulum* (Link) Malte var. *glaucum* (Pease & Moore) Malte [*A. caninum* (L.) Beauv. var. *tenerum* (Vasey) Pease & Moore] P. A. *
*Agrostis alba* L. # M.
*A. scabra* Willd. # M.
*Anthoxanthum odoratum* L. –/–/– M.
*Dactylis glomerata* L. –/–/– M.
*Danthonia compressa* Aust. –/–/– S.
*D. spicata* (L.) Beauv. W. M.
*Deschampsia flexuosa* (L.) Trin. –/–/– M.
*Festuca elatior* L. –/–/– M.
*Muhlenbergia glomerata* (Willd.) Trin. P. M.
*Oryzopsis asperifolia* Michx. E. M.
*O. pungens* (Torr.) Hitchc. E. M.
*Panicum boreale* Nash –/–/– M.
*P. columbianum* Scribn. H.
*P. lanuginosum* Ell. var. *fasciculatum* (Torr.) Fern. –/–/– M.
*P. latifolium* L. W. *
*P. linearifolium* Scribn. W. *
*Phalaris arundinacea* L. –/–/– M.
*Phleum pratense* L. W. M.
*Poa compressa* L. # M.
*P. pratensis* L. H. M.
*Trisetum spicatum* (L.) Richter var. *molle* (Michx.) Beal –/–/– M.

CYPERACEAE

*Carex arctata* Boott –/–/– M.
*C. argyrantha* Tuckerm. [*C. foenea* Willd. var. *perplexa* Bailey] P. M.
*C. brunnescens* (Pers.) Poir. P. *
*C. communis* Bailey E. M.
*C. debilis* Michx. var. *rudgei* Bailey –/–/– M.
*C. intumescens* Rudge –/–/– M.

*C. laxiflora* Lam. W. *
*C. lupulina* Muhl. W. P. M.
*C. projecta* Mackenz. –/–/– M.
*C. scoparia* Schkuhr # M.
*C. trisperma* Dew. # M.
*Eleocharis tenuis* (Willd.) Schultes # *
*Scirpus atrovirens* Willd. H.
*S. rubrotinctus* Fern. –/–/– M.

LEMNACEAE

*Lemna minor* L. –/–/– M.

ERIOCAULACEAE

*Eriocaulon septangulare* With. recorded by "M. A. Coe" in Pease (1911) M.

COMMELINACEAE

*Commelina communis* L. –/–/– M.

JUNCACEAE

*Juncus greenei* Oakes & Tuckerm. –/–/– M.
*J. pelocarpus* Meyer P. *
*J. tenuis* Willd. W. M.
*Luzula multiflora* (Retz.) Lejeune –/–/– M.

LILIACEAE

*Clintonia borealis* (Ait.) Raf. A. *
*Helonias bullata* L. K. *
*Hemerocallis flava* L. –/–/– M.
*Lilium grayi* S. Wats. K. *
*L. philadelphicum* L. W. M.
*L. superbum* L. K. *
*Maianthemum canadense* Desf. W. M.
*Medeola virginiana* L. W. M.
*Polygonatum pubescens* (Willd.) Pursh [*P. biflorum* (Walt.) Ell.] # M.
*Smilacina racemosa* (L.) Desf. A. M.
*Streptopus amplexifolius* (L.) DC. var. *americanus* Schultes –/–/– M.
*Trillium erectum* L. –/–/– M.
*Uvularia sessilifolia* L. [*Oakesia sessilifolia* (L.) Wats.] # *

IRIDACEAE

*Iris versicolor* L. W. M.

*Sisyrinchium montanum* Greene var. *crebrum* Fern. [*S. angustifolium* Mill.] W. M.

ORCHIDACEAE

*Cypripedium acaule* Ait. E. S. T.
*C. arietinum* R. Br. P. E. S.
*Goodyera pubescens* (Willd.) R. Br. –/–/– M.
*G. tesselata* Lodd. [*Epipactis tesselata* A. A. Eat.] A. S.
*Habenaria hookeri* Torr. P. W. *
*H. psycodes* (L.) Spreng. H.
*Malaxis unifolia* Michx. [*Microstylis unifolia* (Michx.) BSP.] A. *
*Spiranthes cernua* (L.) Richard # *
*S. gracilis* (Bigel.) Beck A. T.

SALICACEAE

*Populus deltoides* Marsh. –/–/– M.
*P. grandidentata* Michx. A. M.
*P. tremuloides* Michx. E. M.
*Salix alba* L. H.
*S. bebbiana* Sarg. [*S. rostrata* Richards] A. M.
*S. glaucophylloides* Fern. [*S. glaucophylla* Bebb. var. *angustifolia* Bebb.] H.

MYRICACEAE

*Comptonia peregrina* (L.) Coult. [*Myrica asplenifolia* L.] W. E. M.
*Myrica gale* L. W. M.
*M. pensylvanica* Loisel. [*M. carolinensis* Mill.] W. *

CORYLACEAE

*Alnus rugosa* (Du Roi) Spreng. [*A. incana* (L.) Moench] A. K. M.
*A. crispa* (Ait.) Pursh [*A. viridis* DC.] K. *
*A. serrulata* (Ait.) Willd. W. *
*Betula lenta* L. # K. *
*B. lutea* Michx. f. W. K. M.
*B. papyrifera* Marsh. –/–/– M.
*B. populifolia* Marsh. W. E. M.
*Carpinus caroliniana* Walt. K. M.
*Ostrya virginiana* (Mill.) K. Koch # M.

FAGACEAE

*Fagus grandifolia* Ehrh. # M.
*Quercus alba* L. recorded by "W. H. Ropes" in Pease (1911) M.
*Q. rubra* L. W. M.

ULMACEAE

*Ulmus americana* L. # *

POLYGONACEAE

*Polygonum cilinode* Michx. W. K. M.
*P. persicaria* L. H.
*Rumex acetosella* L. # S. T.
*R. obtusifolius* L. H.

CHENOPODIACEAE

*Chenopodium album* L. –/–/– M.

CARYOPHYLLACEAE

*Cerastium vulgatum* L. H. M.
*Lychnis alba* Mill. –/–/– M.
*Stellaria media* (L.) Cyrillo –/–/– M.

NYMPHAEACEAE

*Nymphaea odorata* Ait. [*Castalia odorata* (Ait.) Woodville & Wood] # *

RANUNCULACEAE

*Anemone virginiana* L. E. M.
*Cimicifuga americana* Michx. K. *
*Clematis virginiana* L. K. *
*Coptis groenlandica* (Oeder) Fern. [*C. trifolia* (L.) Salisb.] A. *
*Ranunculus acris* L. recorded by "M. A. Coe" in Pease (1911) M.
*Thalictrum polygamum* Muhl. # M.
*Xanthorhiza simplicissima* Marsh. [*Zanthorhiza apiifolia* L'Her.] K. H.

BERBERIDACEAE

*Berberis canadensis* Mill. K. *

MAGNOLIACEAE

*Liriodendron tulipifera* L. K. S.
*Magnolia acuminata* L. K. *

*M. fraseri* Walt. K. *
*M. tripetala* L. K. *
*M. virginiana* L. K. *

CALYCANTHACEAE
*Calycanthus floridus* L. K. *

PAPAVERACEAE [FUMARIACEAE]
*Corydalis sempervirens* (L.) Pers. W. M.

CRUCIFERAE
*Brassica rapa* L. [*B. campestris* L.] E. *

SAXIFRAGACEAE
*Hydrangea arborescens* L. H.
*Itea virginica* L. K. *
*Ribes glandulosum* Grauer [*R. prostratum* L'Her.] A. *

HAMAMELIDACEAE
*Hamamelis virginiana* L. W. M.

PLATANACEAE
*Platanus occidentalis* L. K. *

ROSACEAE
*Amelanchier canadensis* (L.) Medic. W. E. [W. specimen looks like hybrid]
*A. laevis* Wieg. –/–/– M.
*A. stolonifera* Wieg. [*A. spicata* (Lam.) K. Koch] W. E. M.
*Fragaria vesca* L. var. *americana* Porter # M.
*Potentilla canadensis* L. –/–/– M.
*P. norvegica* L. [*P. monspeliensis* L.] W. M.
*P. recta* L. –/–/– S. T.
*Prunus pensylvanica* L. f. E. M.
*P. serotina* Ehrh. # M.
*Pyrus melanocarpa* (Michx.) Willd. A. M.
*Rosa blanda* Ait. recorded by "M. A. Coe" in Pease (1911) M.
*R. palustris* Marsh. [*R. carolina* L.] H. M. T.
*R. setigera* Michx. K. *
*Rubus allegheniensis* Porter A. M.
*R. hispidus* L. recorded by "M. A. Coe" in Pease (1911) M.
*R. idaeus* L. var. *aculeatissimus* [C. A. Mey.] Regel & Tiling A.
*R. idaeus* L. var. *strigosus* (Michx.) Maxim. M.

*R. laciniatus* Willd. K. *
*R. odoratus* L. A. S. T.
*Spiraea latifolia* Borkh. W. M.
*S. tomentosa* L. # M.

LEGUMINOSAE
*Apios americana* Medic. [*A. tuberosa* Moench] # *
*Desmodium perplexum* Schub. [*D. dillenii* Darl.] recorded by "M. A. Coe" in Pease (1911) E. H. M.
*Robinia hispida* L. K. H. M.
*Trifolium agrarium* L. W. M.
*T. hybridum* var. *elegans* (Savi) Boiss. H. M.
*T. pratense* L. A. M.
*T. repens* L. W. M.
*Vicia cracca* L. –/–/– M.

OXALIDACEAE
*Oxalis europaea* Jord. –/–/– M.

ANACARDIACEAE
*Rhus radicans* L. [*R. toxicodendron* L.] W. M.
*R. typhina* L. W. M.

AQUIFOLIACEAE
*Ilex glabra* (L.) Gray K. M.
*I. montana* T. & G. [*I. monticola* Gray] K. *
*I. verticillata* (L.) Gray A. M.
*Nemopanthus mucronata* (L.) Trel. E. M.

ACERACEAE
*Acer pensylvanicum* L. A. M.
*A. rubrum* L. A. M.
*A. saccharum* Marsh. # M.

BALSAMINACEAE
*Impatiens capensis* Meerb. [*I. biflora* Walt.] A. M.

VITACEAE
*Parthenocissus inserta* (Kerner) K. Fritsch [*Psedera vitacea* (Knerr) Greene (?)] # M.
*P.* sp. K. *
*Vitis aestivalis* Michx. var. *argentifolia* (Munson) Fern. A. M.

TILIACEAE
*Tilia americana* L. # M.

GUTTIFERAE

*Hypericum canadense* L. –/–/– M.
*H. frondosum* Michx. [*H. aureum* Bart.] K. *
*H. densiflorum* Pursh K. *
*H. majus* (Gray) Britt. H.
*H. perforatum* L. recorded by "M. A. Coe" in Pease (1911) M.
*H. spathulatum* (Spach) Steud. [*H. prolificum* L.] K. *
*H. virginicum* L. A. *

VIOLACEAE

*Viola incognita* Brainerd var. *forbesii* Brainerd W. H. M.
*V. pallens* (Banks) Brainerd # *
*V. renifolia* Gray A. *
*V. septentrionalis* Greene A. M.

NYSSACEAE

*Nyssa sylvatica* Marsh. # M.

ONAGRACEAE

*Epilobium angustifolium* L. A. *
*E. coloratum* Biehler H.
*E. glandulosum* Lehm. var. *adenocaulon* (Haussk.) Fern. [*E. adenocaulon* Haussk.] H.
*E. strictum* Muhl. [*E. densum* Raf.] # *
*Oenothera biennis* L. # *

ARALIACEAE

*Aralia hispida* Vent. # M.
*A. nudicaulis* L. A. M.
*A. racemosa* L. A. M.

UMBELLIFERAE

*Sanicula marilandica* L. H.
*Sium suave* Walt. [*S. cicutaefolium* Schrank] P. M.

CORNACEAE

*Cornus alternifolia* L. f. K. *
*C. canadensis* L. W. M.
*C. rugosa* Lam. [*C. circinata* L'Her.] A. *
*C. stolonifera* Michx. K. *

CLETHRACEAE

*Clethra acuminata* Michx. K. *
*C. alnifolia* L. K. *

PYROLACEAE

*Chimaphila maculata* (L.) Pursh –/–/– M.
*C. umbellata* (L.) Bart. var. *cisatlantica* Blake A. M.
*Moneses uniflora* (L.) Gray –/–/– M.
*Monotropa hypopithys* L. # *
*M. uniflora* L. W. M.
*Pyrola elliptica* Nutt. W. T.
*P. rotundifolia* L. var. *americana* (Sweet) Fern. [*P. americana* Sweet] H. T.
*P. secunda* L. W. *
*P. virens* Schweigger [*P. chlorantha* Sw.] W. M.

ERICACEAE

*Arctostaphylos uva-ursi* (L.) Spreng. A. T.
*Chamaedaphne calyculata* (L.) Moench var. *angustifolia* (Ait.) Rehd. E. M.
*Gaultheria procumbens* L. W. M.
*Gaylussacia baccata* (Wang.) K. Koch A. M.
*G. baccata* (Wang.) K. Koch *forma glaucocarpa* (Robinson) Mackenzie # *
*Kalmia angustifolia* L. W. M.
*K. latifolia* L. K. *
*Leiophyllum buxifolium* (Berg.) Ell. K. *
*Leucothoe editorum* Fern. & Schub. [*L. catesbaei* (Walt.) Gray] K. H.
*Lyonia ligustrina* (L.) DC. # M.
*Oxydendrum arboreum* (L.) DC. K. *
*Rhododendron arborescens* (Pursh) Torr. K. H.
*R. calendulaceum* (Michx.) Torr. K. H. M.
*R. canadense* (L.) Torr. W. E. K. M.
*R. catawbiense* Michx. K. H.
*R. maximum* L. K. M.
*R. roseum* (Loisel.) Rehd. [*R. canescens,* in part, of ed. 7] M.
*R. vaseyi* Gray K. *
*R. viscosum* (L.) Torr. K. M.
*Vaccinium angustifolium* Ait. [*V. pensylvanicum* Lam.] A. M.
*V. atrococcum* (Gray) Heller –/–/– M.
*V. corymbosum* L. # M.
*V. vacillans* Torr. [*V. vacillans* Kalm.] # *

DIAPENSIACEAE

*Galax aphylla* L. K. *
*Shortia galacifolia* T. & G. K. * [not in Fernald, 1950]

PRIMULACEAE

*Lysimachia terrestris* (L.) BSP. # M.

*Trientalis borealis* Raf. [*T. americana* (Pers.) Pursh] A. M. T.

STYRACACEAE

*Halesia carolina* L. K. M.

OLEACEAE

*Fraxinus americana* L. # M.

GENTIANACEAE

*Gentiana andrewsii* Griseb. anonymously reported in Pease (1911) *

*Nymphoides cordata* (Ell.) Fern. [*N. lacunosum* (Vent.) Fern. # *

APOCYNACEAE

*Apocynum androsaemifolium* L. W. M.

*Vinca minor* L. –/–/– M.

ASCLEPIADACEAE

*Asclepias exaltata* L. [*A. phytolaccoides* Pursh] # S.

*A. syriaca* L. –/–/– M.

BORAGINACEAE

*Myosotis scorpioides* L. –/–/– M.

LABIATAE

*Lycopus americanus* Muhl. –/–/– M.

*L. uniflorus* Michx. # M.

*Mentha arvensis* L. var. *villosa* (Benth.) S. R. Stewart [*M. arvensis* L. var. *canadensis* (L.) Briq.] # M.

*Prunella vulgaris* L. # M.

*Pycnanthemum tenuifolium* Schrad. [*P. flexuosum* (Walt.) BSP.] H.

*Scutellaria epilobiifolia* A. Hamilton [*S. galericulata* L.] anonymously reported in Pease (1911) M.

*S. lateriflora* L. H. M.

SCROPHULARIACEAE

*Gratiola aurea* Muhl. # M.

*Melampyrum lineare* Desr. W. M.

*Verbascum thapsus* L. # M.

*Veronica officinalis* L. H. M.

*V. scutellata* L. –/–/– M.
*V. serpyllifolia* L. –/–/– M.

BIGNONIACEAE
*Catalpa bignonioides* Walt. K. *

OROBANCHACEAE
*Epifagus virginiana* (L.) Bart. # M.
*Orobanche uniflora* L. A. *

PLANTAGINACEAE
*Plantago major* L. # M.

RUBIACEAE
*Cephalanthus occidentalis* L. W. K. M.
*Galium tinctorium* L. W. *
*G. triflorum* Michx. # *
*Mitchella repens* L. W. M.

CAPRIFOLIACEAE
*Diervilla lonicera* Mill. A. M.
*D. sessilifolia* Buckl. K. H. M.
*Lonicera canadensis* Bartr. A. M.
*L. japonica* Thunb. var. *halliana* Nicholson K. *
*Sambucus canadensis* L. –/–/– M.
*S. pubens* Michx. –/–/– M.
*Viburnum acerifolium* L. W. M.
*V. alnifolium* Marsh. A. *
*V. cassinoides* L. A. M.
*V. lentago* L. –/–/– M.
*V. recognitum* Fern. [*V. dentatum* L.] W. M.

CAMPANULACEAE [LOBELIACEAE]
*Lobelia cardinalis* L. H.
*L. dortmanna* L. reported by "M. A. Coe" in Pease (1911) *
*L. inflata* L. –/–/– M.

COMPOSITAE
*Achillea millefolium* L. A. M.
*Anaphalis margaritacea* (L.) C. B. Clarke reported by "M. A. Coe" in Pease (1911) M.
*Antennaria canadensis* Greene W. *
*A. fallax* Greene P. *
*A. neglecta* Greene # M.

*A. neodioica* Greene # M.
*A. plantaginifolia* (L.) Hook. E. S.
*Aster acuminatus* Michx. # M.
*A. divaricatus* L. # M.
*A. dumosus* L. # *
*A. macrophyllus* L. P. E. M.
*A. nemoralis* Ait. –/–/– M.
*A. novi-belgii* L. # M.
*A. puniceus* L. # M.
*A. umbellatus* Mill. # M.
*A. undulatus* L. P. M.
*Bidens connata* Muhl. (?) #
*B. frondosa* L. H. M.
*Chrysanthemum leucanthemum* L. –/–/– M.
*Cirsium vulgare* (Savi) Tenore –/–/– M.
*Erechtites hieracifolia* (L.) Raf. H.
*Erigeron canadensis* L. –/–/– M.
*E. strigosus* Muhl. [*E. ramosus* (Walt.) BSP.] # M.
*Eupatorium perfoliatum* L. # *
*E. purpureum* L. # *
*Gnaphalium macounii* Greene [*G. decurrens* Ives] # *
*G. obtusifolium* L. –/–/– M.
*G. uliginosum* L. –/–/– M.
*Hieracium aurantiacum* L. –/–/– M.
*H. paniculatum* L. reported by "M. A. Coe" in Pease (1911) *
*H. pilosella* L. –/–/– M.
*H. pratense* Tausch –/–/– M.
*H. scabrum* Michx. reported by "M. A. Coe" in Pease (1911) S.
*Lactuca canadensis* L. # M.
*Prenanthes trifoliolata* (Cass.) Fern. reported by "M. A. Coe" in Pease (1911) M.
*Rudbeckia serotina* Nutt. –/–/– M.
*Solidago altissima* L. –/–/– M.
*S. arguta* Ait. P. # M.
*S. bicolor* L. A. M.
*S. caesia* L. # M.
*S. canadensis* L. A.*
*S. graminifolis* (L.) Salisb. # *
*S. juncea* Ait. A. M.

*S. nemoralis* Ait. A. M.
*S. rugosa* Ait. # M.
*S. tenuifolia* Pursh –/–/– M.
*Taraxacum officinale* Weber # M.

## DISCUSSION

### Continuity and Change During Eight Decades

A total of 363 species of vascular plants, representing 199 genera and 73 families, has been reported and/or collected on Three Mile Island. Of the species introduced by Kelsey, only the following persist: *Chamaecyparis thyoides, Carpinus caroliniana, Liriodendron tulipifera, Robinia hispida, Ilex glabra, Rhododendron calendulaceum, Rhododendron maximum, Rhododendron viscosum, Halesia carolina,* and *Diervilla sessilifolia.* Most of Kelsey's introductions have disappeared presumably due to intolerance to cold or other climatic/environmental factors.

Since 80% of Kelsey's introductions did not survive, it is instructive to compare geographic ranges of the surviving exotics to the ranges of those not persisting. Of the 10 surviving exotics, 40% naturally reach the latitude of TMI in New England, 20% almost reach the latitude of TMI in New England, 20% range north to Pennsylvania and West Virginia, and 20% range north to Virginia. Thus, 60% of the surviving exotics have been able to survive at TMI in spite of the fact that they are north of their normal ranges. Of the 41 non-surviving exotics, 12% naturally reach the latitude of TMI in New England, 15% almost reach the latitude of TMI in New England, 44% range north to Pennsylvania and West Virginia, 19% range north to Virginia; one is a Rocky Mountain species, two are Old World species, and one (the unidentified *Parthenocissus*) cannot be assigned a range. Of the non-survivors, only 12% might have been expected to survive at the latitude of TMI. Survivorship of Kelsey's introductions was not totally predictable: five northern species that might have been expected to persist did not survive, while six southern species did survive. We might speculate that the microhabitats surrounding each introduction might have been critical in providing the protection necessary to assure survival, but since no location maps of Kelsey's introductions are available, the role of microhabitat must remain speculation.

Table 2. Comparison of native versus adventive species reported at Three Mile Island, New Hampshire, USA, from 1901 to 1985. "Native" is used here to mean indigenous to Three Mile Island, while "adventive" refers to plants from elsewhere in New Hampshire, the United States, and/or Eurasia that have apparently reached the island through human activities.

| | Number of Species | | |
|---|---|---|---|
| Habitat | Persistent [Common to Pease (1911) and to this study] | Lost [Reported only by Pease (1911)] | Influx [Reported only by this study] |
| Native woodland | 91 | 34 | 30 |
| Native open area | 68 | 22 | 21 |
| Native aquatic | 11 | 8 | 6 |
| Adventive | 14 | 1 | 24 |
| Kelsey introductions | 10 | 41 | 0 |

As can be seen from Table 1, we recorded many species new to Three Mile Island. Some species collected only in 1978–85 include: *Chenopodium album, Lychnis alba, Cerastium vulgatum, Stellaria media, Moneses uniflora, Vinca minor* and *Scutellaria epilobiifolia.* In all, 66 species recorded in this study were not included in the 1911 list. An additional 10 species first recorded on Three Mile Island by Hartmann (1941) persist today.

Table 1 compares both species totals and persistence of species on Three Mile Island. General characteristics of plants lost and gained as a group reflect the land use of Three Mile Island, which has been a continuum of small changes spread out over eight decades. Continual influx (and loss) of native woodland species as well as of adventive species account for the two largest changes (Table 2). While the number of adventive ("weedy") species has increased, the number of species indigenous to the islands has remained remarkably constant (Table 2). We suggest that the increase in "weedy" species may be attributed to heavier human traffic (over 1000 people in 1985). "Weedy" adventives are restricted to areas of greatest human use (such as at the main dock and near the central dining facilities). The apparent balance between the number of species reported by Pease (1911) and by this study for "native woodland," "native open area," and "native aquatic" (Table 2) suggests that the numbers of invasions and extinctions have been roughly equal during the last 75 years. In general, we propose that the same niches are available today as

were present 80 years ago, although they may be occupied by different species today.

The Simpson index of resemblance (Simpson, 1965) was used to compare the early taxonomic composition of the total flora of Three Mile Island (Pease, 1911) to the present 1978–85 collection. An index of resemblance was not calculated with the Hartmann list since her collection was limited to a single week (Hartmann, 1941). This index (100c/nl, in which "c" is the number of taxonomic units common to the two floras and "nl" the total number of units in the smaller of the two) seems particularly useful in comparing floras of approximately equal numbers occurring in a single area. The Simpson index of resemblance between the two collections is 0.66. This value falls midway between the lowest (59.2) and highest (72.0) values reported (Lauermann and Burk, 1976) for Penikese Island, part of the Elizabeth Islands chain southwest of Woods Hole, Massachusetts, and suggests that Three Mile Island has experienced a level of disturbance comparable to Penikese.

## Conservation

Botanically the most exciting find during this project was the re-discovery of *Cypripedium arietinum* on August 18, 1985. Earlier that year, Brackley (1985) reported that there was only a single known New Hampshire station for this species. The initial discovery of specimens of Ram's-Head Ladyslipper at Three Mile Island was apparently made during the first botanical exploration of the island on August 17, 1900 (Wilde, 1921). The species flourished well enough during the early twentieth century that 50 blossoms were counted on a botanical trip to the island in 1909 (Richards, 1910). However, by 1985 the population had greatly dwindled in size.

The few individuals left in this colony are growing in close proximity to a popular trail. When the location of the Ram's-Head Ladyslipper was mentioned to concerned campers and island managers, there was general agreement that the location should be protected as best as possible. The Land Use Plan adopted by the Three Mile Island Camp Committee in 1973 has undoubtedly been instrumental in protecting this and other rare species (Maciejowski et al., 1981; Holland et al., 1983), and it is expected that this management plan will continue to provide the

adequate flexibility combined with sufficient rigor needed to promote wise stewardship of the island's natural resources.

The land use plan is ecological in nature and was derived from a compartment model of the basic kinds of environment required by humans (adapted from Odum, 1969). Land areas on islands owned by the Appalachian Mountain Club were classified (Holland et al., 1983) into four major categories of environment utilized by humans:

1. Protective—contain unusual vegetation or natural formations and are generally undeveloped. Under the plan, these areas are most restricted from future development.

2. Compromise—consists of land areas containing a small density of buildings and located along areas of shoreline. While no new building is encouraged, replacement building, trail maintenance, and cutting of vegetation to maintain vistas and to protect buildings are allowed.

3. Productive—designed for forestry and wildlife habitat, improvement cuttings, and managed for the harvest of firewood.

4. Urban—consists of existing built-up areas and areas of heavy use. Although these areas have been used intensively over the years, it is recommended that future construction be approved by an outside review board within the Appalachian Mountain Club.

In adopting these land use recommendations, the Camp Committee stipulated that any new plans for construction within the Urban or Compromise areas must be submitted with a simple environmental impact statement outlining the cost of the proposed project in terms of alteration of the natural state of the area in question. The land use plan was primarily drafted as a guide for the committee to use when planning for future improvements such as cabins, or recreational facilities. However, the plan also helped to resolve a land use conflict which existed at the time the plan was developed. While most people affiliated with Three Mile wanted to preserve the natural state of the island to the fullest possible extent, a conflict arose when proposals were made to increase total number of campers during the island's ten-week season to offset the higher costs of operation. Although the number of campers did not increase, the land use plan provided alternatives for orderly development while maintaining maximum protection of the island's natural state (Sackett and Maciejowski, 1977).

Since its inception in 1972, the land use plan has proven to be a workable framework for maintaining the natural character of Three Mile Island. The designers of the land use plan envisioned a flexible structure, which would allow for minor amendments and additions when necessary. In October of 1985, after the rediscovery of the Ram's-Head Lady Slipper, the Camp Committee agreed to designate the site of the Ram's-Head Lady Slipper a "Protective" area, and thus to continue its commitment to preserve the natural biota of Three Mile Island.

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RHODORA, Vol. 91, No. 868, pp. 339–341, 1989

# NEW ENGLAND NOTE

# ON THE OCCURRENCE OF *ARISAEMA DRACONTIUM* IN HAMPSHIRE COUNTY, MASSACHUSETTS

LAURIE L. SANDERS

**ABSTRACT**

*Arisaema dracontium* (L.) Schott has been historically considered rare in Massachusetts. Recent field studies in selected floodplain forests in Hampshire Co. indicate that *A. dracontium* is more abundant than was previously believed.

Key Words: *Arisaema dracontium,* floodplain forests, Hampshire Co., Massachusetts

Green dragon, *Arisaema dracontium* (L.) Schott (Araceae), was historically considered rare in Massachusetts (Williams, 1910; Livingston, 1964) and is currently listed as "threatened" (Sorrie, 1987) in the state. This apparent scarcity has probably been caused by the extensive conversion of floodplain forest and alluvial meadows into cropland (Sorrie, 1987).

Previously known from nine locations in Hampshire Co., Massachusetts, *Arisaema dracontium* was located and last collected along the Connecticut River in Northampton by H. E. Ahles in 1978 (*Ahles 86320,* MASS). Subsequent attempts to re-locate this station, however, were unsuccessful (B. Sorrie, pers. comm.; M. Rohman, pers. comm.). As of spring, 1988, only one extant Hampshire Co. population of *A. dracontium,* comprised of a few individuals along the Mill River in Northampton, was known (J. Anderson, pers. comm.).

During June, 1988, I attempted to locate populations of *Arisaema dracontium* by making thorough searches of Connecticut River floodplain forests and their borders in Hampshire Co. After re-locating two historic populations in Northampton, I noticed that they shared distinct similarities in their surrounding flora and in their location with respect to flood levels and topographic features.

Within and bordering the floodplain forest communities, *Arisaema dracontium* was observed growing in the narrow transition zone between those areas which remain wet later into the summer and the drier uplands. Green dragons were found rimming the depressions which act as temporary pools, as well as in low spots

on river terraces and amidst tree falls where flood debris had accumulated.

Using this information, I consulted U.S.G.S. topographic maps in order to identify similar floodplain forests. By combining these map data with historical records and field work, seven distinct populations were found.

The *Arisaema dracontium* populations were found along the floodplain of the Connecticut River in Hatfield (1), Hadley (1), and Northampton (4), and along the Mill River floodplain in Northampton (1). Five are new stations. Two of these stations contain over 500 blooming individuals and are therefore among the largest populations in the state.

The soil type at most of the sites was either Limerick silt loam or Hadley silt loam (Swenson, 1981). In adjacent floodplain forests characterized by Winooski silt loam or Suncook loamy, fine sand, such as Rainbow Beach in Northampton and west of Mitch's Marina in Hadley, MA, no *Arisaema dracontium* was found.

With few exceptions, *Arisaema dracontium* was growing in areas which were sparsely vegetated. Associated understory plants nearby were *Onoclea sensibilis* L., *Matteuccia struthiopteris* (L.) Todaro, *Impatiens capensis* Meerb., *Apios americana* Medic., *Boehmeria cylindrica* L., *Vitis* sp., *Parthenocissus quinquefolia* (L.) Planch., *Laportea canadensis* (L.) Wedd., *Lysimachia ciliata* L., *L. nummularia* L., *Arisaema triphyllum* var. *stewardsonii* (Britt.) Stevens, *A. triphyllum* var. *triphyllum* (L.) Schott, *Rhus radicans* L., *Smilax herbacea* L., and *Sambucus canadensis* L. The overstory was usually dominated by *Acer saccharinum* L.; other canopy trees were *Salix nigra* Marsh., *Populus deltoides* Marsh., and *Fraxinus pennsylvanica* Marsh.

*Arisaema dracontium* is therefore more abundant in Hampshire Co. than previously believed. Whether these newly located populations represent old established populations formerly overlooked or are the result of an expansion of *A. dracontium* within its range is presently unknown.

## ACKNOWLEDGMENTS

I express my appreciation to B. Sorrie for suggesting that I search for *Arisaema dracontium* and for providing historical information, to F. Morrison and C. J. Burk for their helpful comments on this manuscript, and to the Maggie Walsh Grantham

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# NEW ENGLAND NOTE

# SOME NEW RECORDS FOR NEW ENGLAND AND NEW ENGLAND STATES

RAY ANGELO

This note is intended to be the first in a series of occasional notes that will report new state records for New England that come to the attention of the Club's Curator of Vascular Plants in the course of his curatorial duties. All records cited here are for specimens that have been accessioned by the Club herbarium (NEBC). Their newness has been determined by making use of the most current floras, checklists and other readily available published sources that are based upon herbarium records.

## New Records for New England

*Allium sativum* L.—Chilmark, MA (Dukes Co.); Frank C. MacKeever (MV483); July 18, 1961; "old waste area."

*Caragana arborescens* Lam.—Concord, MA (Middlesex Co.); Ray Angelo and Sarah Chapin; May 18, 1983 (flowers), Aug. 21, 1983 (fruit); "Pratt area southwest of Punkatasset Hill. Rich thicket. Well established with many seedlings. Shrubs up to 2 m high. Flowers yellow. Material collected from same plant. Station since destroyed by bulldozer."

*Syringa amurensis* (Rupr.) Rupr.—Concord, MA (Middlesex Co.); Ray Angelo and John Dolan (flowers), Sarah Chapin (fruit); June 24, 1983 (flowers), Oct. 9, 1983 (fruit); "Pratt area SW of Punkatasset Hill. Rich woods along trail. Well established with many seedlings. Shrubs up to 5 m high. Flowers white. Material collected from same plant." [Station since destroyed by land improvement operations.]

## New Records for New Hampshire

*Menispermum canadense* L.—Westmoreland, NH (Cheshire Co.); D. E. Boufford (#23921), J. Murata, H. Ohashi and E. Wood; June 19, 1988; "near the confluence of Aldrich Brook and the Connecticut River just along the town line with Walpole. Elev. ca. 80–85 m. With *Acer saccharinum, Platanus,*

*Tilia,* etc. Twining vines (all staminate) 1.5–2 meters long in thicket on south side of Aldrich Brook; flowers white, pollen yellow."

*Alliaria petiolata* (Bieberstein) Cav. & Grande [syn. *A. officinalis* Andrz.]—Cornish, NH (Sullivan Co.); D. E. Boufford (#23930), H. Ohashi and E. Wood; July 5, 1988; ".32 km (.2 mi.) NW of New Hampshire Route 12-A on Ferry Hill Road. Elev. ca. 95–100 m. Roadside, rich soil at edge of deciduous forest. Colony of 50 or more individuals. Crushed plants with odor reminiscent of garlic."

*Celastrus orbiculatus* Thunb.—Chesterfield, NH (Cheshire Co.); D. E. Boufford (#23648) and E. W. Wood; May 25, 1986; "village of West Chesterfield, just north of the village on River Road. Elevation ca. 90 m. Sandy loam alluvial soil along the Connecticut River. Woody vine about 5 m tall; growing in thicket between River Road and river; flowers greenish."

## New Records for Vermont

*Nardus stricta* L.—Victory, VT (Essex Co.); D. E. Boufford (#22951) and D. S. Conant; June 14, 1982; "south of the village of Victory on the road to North Concord; 8.16 km (5.1 mi.) north of the confluence of Moose River and Bog Brook along Moose River. Elev. ca. 375 m. Growing in sand in clearing on upper part of riverbank."

*Thermopsis villosa* (Walt.) Fern. & Schub.—Dummerston, VT (Windham Co.); L. A. Charrette (#3345); June 28, 1969; "In the north section of the town of Dummerston. Just south of the boundary line of the towns of Putney and Dummerston. Along highway embankments of U.S. Route No. 5. This area (abounding in many unexpected exotics with appearance of being well established) is a section of Route 5 which was re-routed through a commercial plant nursery. Quite numerous on east side of highway on top of embankment at edge of woodlands." [This specimen identified as *Thermopsis mollis* by collector; annotated as *T. villosa* by Ray Angelo. This species also collected by same collector from Putney, VT on same day (#3349).]

*Lactuca muralis* (L.) Gaertner—Brattleboro, VT (Windham

Co.); F. Koch; Aug. 3, 1979; "1.4 miles on Black Mtn. Road west of intersection with U.S. Rte. 5. Mixed hardwoods."

**New Records for Massachusetts**

*Thermopsis villosa* (Walt.) Fern. & Schub.—Framingham, MA (Middlesex Co.); H. E. Ahles (#80370); June 27, 1975; "wooded road bank, Mass. Pike exit to Rte. 9." [Also collected from Lincoln, Middlesex Co. (R. Angelo and P. Walker, 1979), Wilmington, Middlesex Co. (D. E. Boufford (#23650) and E. W. Wood, 1986), and Goshen, Hampshire Co. (B. A. Sorrie (#1571), H. L. Woolsey, G. M. Flatebo, 1982).]

*Linaria maroccana* Hook. f.—Concord, MA (Middlesex Co.); Ray Angelo and Dorian Kottler; Aug. 24, 1985; "Recently cleared area (formerly woods) near Sudbury River above Hubbard Bridge about ¼ mile north side between house and river. At least a dozen plants. Flowers violet with yellow or orange spot." [Also collected from Cambridge, Middlesex Co. (R. Angelo and D. Kottler, 1986).]

*Lactuca muralis* (L.) Gaertner—Lincoln, MA (Middlesex Co.); Ray Angelo and Dorian Kottler; July 1, 1984; "Plentiful at edge of woods and parking lot of DeCordova Museum. Flowers yellow."

**New Records for Rhode Island**

*Malaxis unifolia* Michx.—Diamond Hill (Town of Cumberland), RI (Providence Co.); E. J. Palmer (#46728); July 31, 1943; "Swampy woods between rocky hills and brook."

NEW ENGLAND BOTANICAL CLUB HERBARIUM
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CAMBRIDGE, MA 02138

## NEBC AWARD
## FOR THE SUPPORT OF BOTANICAL RESEARCH

Mr. Scott Shumway, Biology Department, Brown University, Providence, Rhode Island, was selected to receive the 1989 New England Botanical Club Award in support of botanical research for his proposal, "Population genetics of a founder species in an incipient salt marsh."

The New England Botanical Club will again offer an award of $1000 in support of botanical research to be conducted in relation to the New England flora during 1990. This award is made to stimulate and encourage botanical research on the New England flora and to make possible visits to the New England region by those who would not otherwise be able to do so. The award will be given to the graduate student submitting the best research proposal dealing with field studies in systematic botany, biosystematics, and plant ecology, but proposals for research in other areas of botany will also be considered. This award is not limited to graduate students at New England institutions, nor to members of the New England Botanical Club. Papers based on this research must acknowledge the NEBC's support, and it is encouraged that they be submitted to *Rhodora,* the Club's journal, for possible publication—subject to standard review processes.

Applicants should submit a proposal of no more than three double-spaced pages, a budget (the budget will not affect the amount of the award), and a curriculum vitae. Two letters, one from the student's major professor, in support of the proposed research are also required. Proposals and supporting letters should be sent before 28 February 1990 to:

Awards Committee
The New England Botanical Club
22 Divinity Avenue
Cambridge, MA 02138

The recipient of the award will be notified by 30 April 1990.

# THE 1989 JESSE M. GREENMAN AWARD

The 1989 Jesse M. Greenman Award has been won by Carol A. Todzia for her publication "Chloranthaceae: *Hedyosmum,*" which appeared in Flora Neotropica Monographs, Volume 48. This monograph is derived from a Ph.D. dissertation submitted to the University of Texas, under the direction of Dr. Beryl B. Simpson. The genus *Hedyosmum* is comprised of 40 species of predominantly montane, neotropical shrubs and trees. The comprehensive monograph, which includes four newly described species, reexamines previous treatments of the genus and presents new data on anatomy, morphology, ecology, and geography. Synopses of the taxonomic history, palynology, cytology, and uses are also provided.

This Award is named for Jesse More Greenman (1867–1951), who was Curator of the Missouri Botanical Garden Herbarium from 1919 until 1943. A cash prize of $500 is presented each year by the Garden, recognizing the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year.

Nominations for papers published during 1989 are now being accepted for the 22nd annual award, which will be presented in the summer of 1990. Reprints of such papers should be sent to:

Greenman Award Committee
Research Division
Missouri Botanical Garden
P.O. Box 299
St. Louis, MO 63166-0299, U.S.A.

In order to be considered for the 1990 award, reprints must be received by June 1, 1990.

# REVIEWERS OF MANUSCRIPTS
# JULY 31, 1988–JULY 31, 1989

The editors of RHODORA are grateful to each of the following specialists for their participation in the review process.

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The New England Botanical Club is a non-profit organization that promotes the study of plants of North America, especially the flora of New England and adjacent areas. The Club holds regular meetings, has a large herbarium of New England plants, and a library. It publishes a quarterly journal, RHODORA, which is now in its 91st year and contains about 500 pages a volume.

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*Sabatia kennedyana* Fern. (Plymouth Gentian). A globally rare, disjunct species of the coastal plain of North America, occurring in northeastern South Carolina, southeastern North Carolina, southeastern New England, and Yarmouth County, Nova Scotia. Original artwork by Tess Feltes; from *New England's Rare, Threatened and Endangered Plants*. Crow, G. E. 1982. Reproduced by permission.

# DR. HERMAN ROYDEN SWEET

## A DEDICATION

This volume of RHODORA is respectfully dedicated to Dr. Herman R. Sweet on the occasion of his retirement as Treasurer of the New England Botanical Club after twenty-three years of faithful service. Dr. Sweet first joined the NEBC in 1938, while he was an Instructor at Tufts University. He was an active member of the Club for many years before assuming the office of Treasurer in 1967, a duty which carried with it the then implicit title of Business Manager of RHODORA. Under his guidance, the endowments of the Club increased threefold at a time when inflation and steeply rising costs of publication of RHODORA took an ever-increasing bite out of the Club's income. He has always been a modest man, willing to be of help and service to the Club and to Club members; many of the actions he took were known only to himself and the particular beneficiary of the effort. He kept up with the tasks of annual billing and collection of membership dues, all address changes, and all claims for lost journal numbers by himself. He was an efficient guardian of the Club's Treasury, and no money was spent without explicit authorization from the Council accompanied by an explanation of why it so voted. He kept up the grand tradition of continuity established by past treasurers, as he was only the fourth treasurer to serve the Club in its nearly 100 years of existence.

A Massachusetts native, Dr. Sweet was born in Attleboro. He received his B.A. from Bowdoin College in 1931, his A.M. from Harvard in 1934, and his Ph.D. from Harvard in 1940. He became an Instructor at Tufts University in 1937, and remained there until his retirement in 1975 as Professor of Biology. At Tufts he taught a wide variety of courses at all levels of instruction, including a highly popular course in ornithology and another in orchidology. His major responsibilities lay with teaching botany to the rather large (350) freshman classes, at which he was an acknowledged master. He also offered two courses in bacteriology (one for 30 years and the other an overlapping 10 years) and a course in microbiology (for more than 30 years). Late in his career, he offered a new "Plants and Man" course which he continued to teach for more than 10 years during summer sessions after his formal retirement.

In 1940, Dr. Sweet began to study orchids, a plant group which had fascinated him since early childhood. In 1949, he built a

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greenhouse at his home and began to grow orchids on a quite respectable scale. Orchids were as important to him as his teaching, and Dr. Sweet was involved in every phase of them—their taxonomy, their cultivation, horticultural aspects of their propagation, and the judging of specimens and new hybrids at orchid shows. In 1952, he was a founder of the Massachusetts Orchid Society, serving as its Secretary-Treasurer until 1958 and its President from 1958–60 and again during 1964–65. It was Dr. Sweet who was responsible for setting up the standards and requirements for orchid judging, and who, along with Helen Adams, a grower from Wellesley, Massachusetts, wrote the definitive manual of instructions for orchid judges. From 1954 to 1961, Dr. Sweet was Associate Editor of the American Orchid Society Bulletin, and from 1961–66, he was the Awards Coordinator for the Society. From 1968–74, he served the American Orchid Society as one of its elected Trustees.

In 1965, Dr. Sweet accepted an appointment as Research Associate at the Orchid Herbarium of Oakes Ames at Harvard University, an appointment which he still holds. In this position, he has once more demonstrated his remarkable powers of concentration. He has published about 100 scientific papers on orchids, numerous notes of horticultural import, and four books. The last of these, entitled "The Genus *Phalaenopsis,*" was undertaken by invitation from the Royal Horticultural Society in England. His abiding major interest among the orchids remains, however, the genus *Miltonia,* commonly known as Pansy orchids. Over the years, Dr. Sweet has traveled widely, visiting many orchid collections in Europe and including not only most of the herbaria of North and South America where orchids are studied, but as well, most of the private horticultural growers in these areas. In 1967, he was elected a Fellow of the Linnean Society of London, and in 1978, a member of the Explorers Club. He has collected every stamp issued world-wide which features an orchid. His library contains some of the rarest and most beautiful books which deal with orchids. He is, in short, a modern version of the Renaissance Man and a true gentleman in every noble sense of the word. We are genuinely fortunate for his long service as NEBC Treasurer; his counsel and reliable attention to day-to-day details have helped make the Club a first-rate organization, and he will be sorely missed. Herman, we salute you and in all sincerity, wish you well.

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# THOMAS F. LUCY'S "UPPER SUSQUEHANNA FLORA" HERBARIUM REDISCOVERED

CAROL L. KELLOFF,[1] LEE B. KASS, AND ANTHONY J. KOWALSKI[2]

## ABSTRACT

Thomas F. Lucy's original herbarium of "The Upper Susquehanna Flora," fully mounted and labeled for the Elmira Academy of Sciences in the 1890's, has been found at Elmira College. Although *Index Herbariorum* indicates that BUF contains the largest deposit of the collections of T. F. Lucy, these specimens are Lucy's unmounted duplicates. T. F. Lucy did not die in Elmira, as earlier reported, but had moved to Buffalo and died there in 1906. Based on Lucy's collection, a working herbarium has been established in Carnegie Science Hall at Elmira College. Current research is focusing on updating Lucy's obsolete nomenclature, mapping the localities and collection sites, and identifying the duplicate specimens from BUF.

Key Words: Thomas Francis Lucy, The Upper Susquehanna Flora, Elmira Academy of Sciences, Elmira College Herbarium, New York

## INTRODUCTION

In 1984 we discovered an herbarium in a storage room in the Kolker Science Building at Elmira College, Elmira, New York (Long et al., 1987). Close examination revealed that most of the 2200 specimens were collected by Thomas F. Lucy, M.D. Heading Lucy's meticulously detailed, handwritten labels was the typeset title, "The Upper Susquehanna Flora, Elmira Academy of Sciences." We began our investigation by consulting Barnhart's (1965) *Biographical Notes upon Botanists*.

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## THOMAS FRANCIS LUCY

Thomas Francis Lucy was born in Worcester, England, on 7 June 1844 (*Chi Phi Centennial Memorial Vol.,* 1924), the son of Henry and Sarah Hook Lucy (Bureau of Vital Statistics–Buffalo, 1906). At the time of the 1860 U.S. Census, Lucy, his mother, and two siblings were living in Corning, NY. At age 21, he attended Hobart College, Geneva, NY (*Catalogue of Hobart College,* 1865–66), and received his M.D. from the Eclectic Medical College in New York City at age 37 (Weaver, 1890). Lucy married, moved to Chemung County and at the time of the 1880 Census was settled in Elmira, NY. Upon examining the Elmira City Directories, we found that Lucy was listed as a physician in 1887. Between 1881 and 1889 he was a member of the American Society of Microscopists (Weaver, 1890; *Chi Phi Centennial Memorial Vol.,* 1924), the Genesee Valley Eclectic Medical Society (Weaver, 1890) and the Elmira Academy of Sciences (1881). Sometime around 1900 Lucy moved out of Elmira; we found him listed in the 1901 Buffalo City Directory. Lucy died in Buffalo on 29 October 1906 of Bright's Disease (Bureau of Vital Statistics–Buffalo, 1906). A detailed biography is currently in preparation.

## THE LUCY COLLECTIONS

From *Index Herbariorum* (Chaudhri et al., 1972) we learned that Lucy's collections should be housed in the Field Museum of Natural History in Chicago (F), the University of Minnesota Herbarium (MIN), the Herbarium of the New York Botanical Garden (NY), and the New York State Museum Herbarium (NYS). The *Index* lists the Buffalo Museum of Science (BUF) as the main repository for his collection, but does not mention Elmira College. We visited BUF in March, 1986, and found what appeared to be unmounted duplicates of the specimens we had found at Elmira College. These specimens were still in the original newspapers used by Lucy and tied into bundles. Within each bundle, numbers were found penciled along the edges of some newspapers. In most cases this number was the only identification of a particular specimen and of the next few un-numbered specimens. To the curators at BUF, these numbers had no significance. Comparison of these numbers with the Patterson (1892) and Heller (1898) check-list numbers found on the herbarium labels of the Elmira College

Flora of the Upper Susquehanna.

DECEMBER, 1899.

The recent publication of the Flora of the Susquehanna, by Mr. Willard N. Clute, of the Botanical Garden, has brought to the notice of American botanists, for the first time, the distribution of the species therein enumerated for this region of the state. Having assisted in the botanical work therein outlined, and having for the past thirty years been particularly interested in the Flora of the Chemung River Valley, and the smaller streams tributary to it, which has resulted in a critical study of this flora and also the collection of a large number of duplicate species, all the more critical ones of which having been determined by comparison at the Herbariums of Columbia University and the Botanical Garden, New York City, the undersigned is prepared to offer specimens, carefully prepared and labeled, of the above Flora at the rate of Five Dollars per 100 species, charges for less than 100 in accordance with rarity of species selected. Less than fifty at 10c. per specimen, purchasers to pay their own transportation charges.

Lists of species per Patterson's or Heller's check list as desired.

Address

THOMAS FRANCIS LUCY, M. D.,

215 Mt. Zoar Street, Elmira, N. Y.

Figure 1. Photocopy of the flyer distributed in 1899 advertising for sale, at the rate of five dollars per 100 species, duplicate specimens of the *Flora of the Upper Susquehanna,* listed per Patterson's or Heller's check list (Smithsonian Institution Archives).

specimens verified that most of the numbers used in the BUF collection referred to Patterson's Check List. Apparently Lucy was using the Patterson and Heller numbers as a shorthand reference to his duplicate specimens. Some label information was found within these bundled specimens, but it was incomplete. Most specimens contained no label information at all. With some of the specimens, Lucy had placed a small slip of paper with the

location and date written in an abbreviated form. For locations in the city of Elmira or Sullivan Hill, he would write "city" or "Sul." For the most part, the dates appear as "1886" or "86." The few completed labels found with the specimens at BUF varied in design and did not have the extensive information that we found so frequently in the collection at Elmira.

Labels found at MIN and at the Smithsonian Institution herbaria (US) were similar to those located at BUF. According to the old record books at MIN, the herbarium received 266 specimens from Lucy between 1895 and 1898. Gerald B. Ownbey, former curator at MIN, believes that these specimens were sent unmounted since the specimens are mounted on paper used at MIN in the 1890's. "The labels are . . . the ones that came with the specimens and are unaltered" (letter from G. B. Ownbey to C. Long, 4 Nov., 1986). The specimens found at US had been acquired through an exchange with NY. These specimens had also been mounted on paper used at US. Inquiries to the archives of MIN, NY, NYS and BUF could not supply us with any additional information, but a reply from the archivist at US clarified the reason why so many duplicates were found at BUF. Among the documents received was a printed flyer dated December 1899, advertising that Lucy had for sale duplicate specimens from the Flora of the Upper Susquehanna (Figure 1). These specimens, Lucy indicated in the flyer, could be referenced to "Patterson's or Heller's check-list as desired" (Smithsonian Institution Archives). On the basis of the knowledge of this flyer and our research revealing that Lucy had moved to Buffalo ca. 1900 and died there in 1906, we confirmed our belief that the specimens at BUF were indeed Lucy's duplicates.

## THE UPPER SUSQUEHANNA FLORA

When Willard Nelson Clute started working on his *Flora of the Upper Susquehanna and its Tributaries* (1898), nothing had been published on the flora around the headwaters of the Susquehanna River. For help with his floristic survey, Clute turned to the botanists of the area: W. C. Barbour, S. A. Brown, F. V. Coville, F. E. Fenno, J. A. Graves, D. F. Hoy, C. F. Millspaugh, and T. F. Lucy. *The Flora of the Upper Susquehanna* was important as it was the "connecting link between the 'flora of the Lackawanna and Wyoming Valleys' [Dudley and Thurston, 1892] and the

'Cayuga Flora' [Dudley, 1886] and thus complet[ed] the chain of local floras extending from eastern Pennsylvania to Lake Ontario" (Clute, 1898). Its preface stated that Lucy devoted 30 years to collecting plant specimens of the Chemung Valley, and toward the end of the 1890's, Lucy presented to the Elmira Academy of Sciences "a nearly complete collection of the plants of our region" (Clute, 1898). This "nearly complete collection" is the one now in our possession.

## THE ELMIRA ACADEMY OF SCIENCES

The Elmira Academy of Sciences was established in 1861 as a society for "the pursuit of astronomical and scientific studies" (Elmira Academy of Sciences, 1881). It was housed in the Observatory (Figure 2), which was located across from the Elmira Female College (name changed to Elmira College in 1890; Barber, 1955). In 1881, the Elmira Academy of Sciences "turned the observatory over to the [Elmira Female] college, complete with its excellent equipment and a wonderul heritage" (Barber, 1955). *The Forty-Fourth Annual Catalogue of Elmira College* (1898–99) reports that the Observatory also contained a museum which housed many natural history collections. It may have been in the Observatory's museum that the plant collection was originally housed. According to the charter of the Elmira Academy of Sciences (1881, 1897), Lucy was the chairman in its Section of Botany. The first mention that the College has an herbarium of plants of "Elmira and vicinity" is found in the *Forty-Fifth Annual Catalogue of Elmira College* (1899–1900) as a description for the "new museum" under the heading for Botany. This same entry reports that an additional "large exhibit is expected in the near future." We assumed this "large exhibit" was the collection Lucy gave to the Elmira Academy of Sciences. The 1900 *Sibyl,* then Elmira College's news magazine, and a letter dated "Oct 6-1900" from Lucy to Charles Peck, State Botanist, Albany, NY, confirmed our assumption. The *Sibyl* provided us with a full description of this "new museum" and its founder, Dr. Darius R. Ford. "The collection in botany" is described as having specimens which "are beautifully mounted, and are classified and determined after the latest botanical nomenclature. The principle [sic] collection is due to the interest of Dr. T. F. Lucy, of Elmira, . . ." (Brooks, 1900). The Lucy letter states, "There are probably over

Figure 2. Photograph of the Elmira Academy of Sciences' Astronomical Observatory, begun in 1858–59, and located across from the Elmira Female College. The Academy held their meetings in the Observatory building. In 1881 the building was turned over to the college; it was razed in 1939.

1500 mounted sheets now deposited in the Ford museum at Elmira [College]." We presume that prior to the Observatory's razing in the summer of 1939 (Pott, 1939), the rest of the contents of the Observatory's museum was moved to the Ford Museum in Gillett Hall (*Forty-Fifth Annual Catalogue of Elmira College,* 1899–1900), the music building of the Elmira Female College. The Ford museum is no longer in existence, and how the herbarium collection came to be housed in the Kolker Science Building is yet unknown. However, we assume that the herbarium was brought to Kolker shortly after the building was erected in the 1950's.

Of the 2200 specimens in the collection found in Kolker, 1160 were collected by Lucy. These specimen labels have quite extensive information. Along with the collection number, scientific name, locality, habitat, geographical distribution and date, Lucy included cross references to Britton and Brown's (1896–98) first edition of an *Illustrated Flora*; Patterson's (1892) *Numbered Checklist*; Heller's (1898) numbers from the *Catalogue of North American Plants*; and finally (in the bottom right hand corner) the number from Durand's (1887) *Index Generum Phanerogamorum*

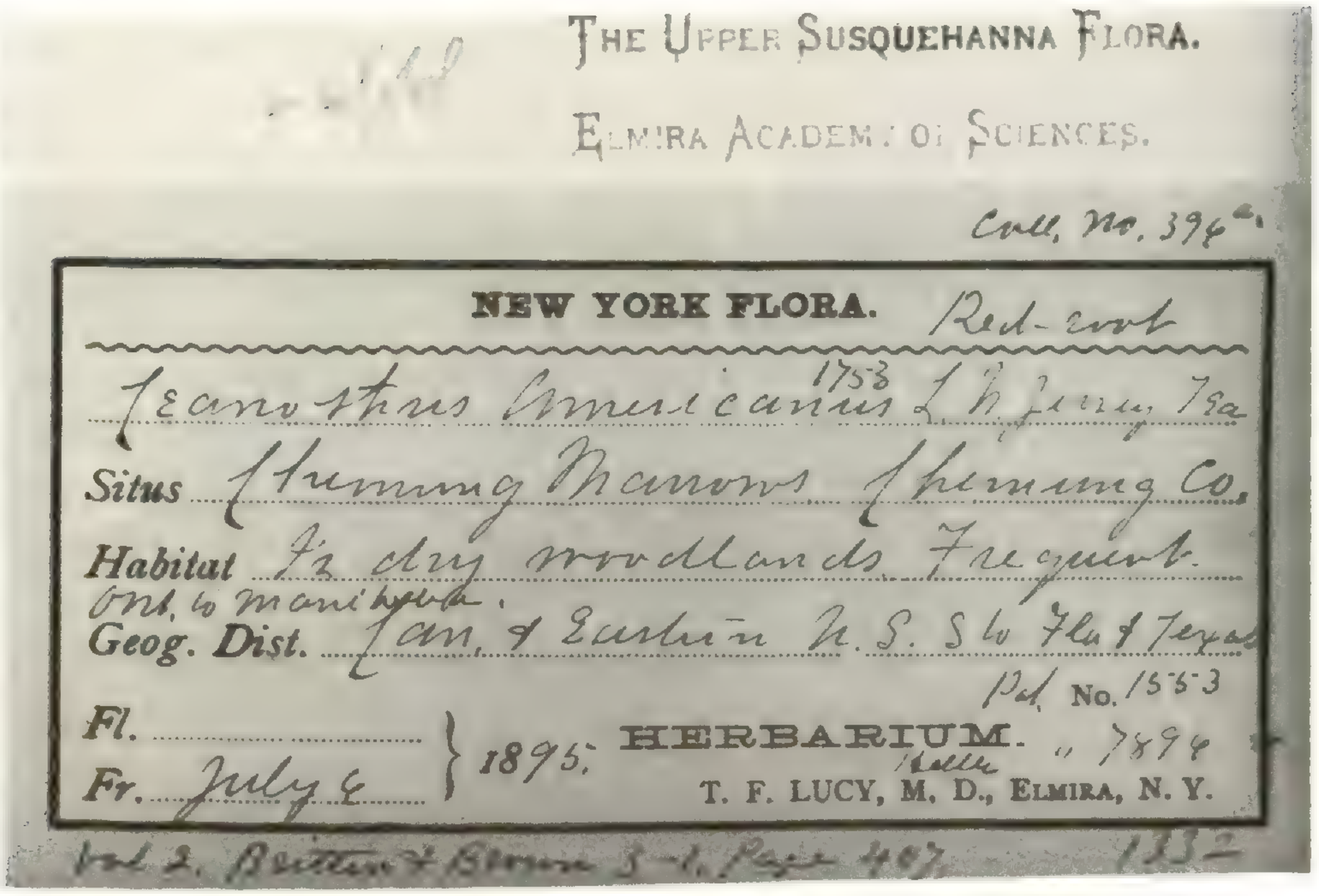


Figure 3. Photograph of a typical label found in the Lucy herbarium collection at Elmira College. Lucy's collection number appears on the upper right of the label. The Patterson (1892), Heller (1898) and Durand (1887) numbers appear on the lower right. Across the bottom of the label is found reference to the first edition of Britton and Brown (1896–98). Note the typeset title above the label, The Upper Susquehanna Flora, Elmira Academy of Sciences, and the annotation initials of Stanley J. Smith to the left of title.

(Figure 3). As if this were not enough, other information such as synonyms, subspecies, varieties, and the common name were often recorded around the borders and squeezed in between the lines.

Another interesting aspect of the Academy's collection was the multiple labels found on some of the specimens. When Lucy mounted a specimen collected by another botanist, he always affixed his own label in the lower right corner, complete with information and cross-referencing (but excluding the collection number) and placed the original collector's label in the lower left. In some cases where specimens of the same species were collected separately by two botanists, the plants were mounted together on one sheet and a third label was added to the top right corner of the herbarium sheet. Additionally, in 1945, either annotation labels or handwritten initials (Figure 3) of Stanley J. Smith (who became curator of NYS), were affixed above or to the left of Dr. Lucy's labels. Apparently, Smith, then a graduate student at Cor-

nell, studied and reclassified many of the specimens in Lucy's collection (Anon, 1945a, 1945b).

## THE ELMIRA COLLEGE HERBARIUM

The Academy's herbarium collection has been relocated to the newly established Elmira College Herbarium in Carnegie Hall. This collection has been extensively renovated, alphabetized by family, and repaired where needed. Label information has been compiled on a computer database (IBM PC-File III) for easy reference. The collection has been housed along with collections of New York State flora, donated by Dr. Peter Hyypio, former curator of the Bailey Hortorium (BH) at Cornell University, Dr. Herman Forest, curator of the Herbarium of SUNY Geneseo (GENU), as well as by Elmira College students.

The Elmira College Herbarium is currently used as both a research and a teaching herbarium. Along with curating the existing collection, current research by both undergraduate and graduate students is focusing on updating the obsolete nomenclature, mapping the localities of the collection sites, identifying the specimens from BUF, and incorporating many of them into the Elmira College Herbarium. We welcome use of this resource by other botanists.

## ACKNOWLEDGMENTS

We thank the following people for their help and encouragement during this project: Dr. Steve Clemants, former New York Natural Heritage Program Botanist, for locating information on Dr. Lucy at the New York State Museum, Albany; Robert Dirig, Assistant Curator of BH, for continued support throughout this task and for help with manuscript preparation; Dr. Richard Eyde, Curator, Dept. of Botany, Smithsonian Institution, for help with ms. preparation; Dr. Leonard Grant, former President of Elmira College, for travel assistance to visit BUF; Dr. Peter Hyypio, former Curator of BH, for initial help with locating references on Dr. Lucy; Jan Kather, Elmira College Photographer/Graphic Artist, for help with photographic reproductions; Dr. Malcom Marsden, Elmira College Dana Professor of English, for historical guidance and help with ms. preparation; Dr. Herbert Wisbey, Jr., former Cu-

rator of the Elmira College Archives, for help with initial information on the Elmira Academy of Sciences; Mark Woodhouse, Reference Librarian and Curator of the Elmira College Archives, for help with locating information on the Ford Museum; Richard Zander, Curator of BUF, for help with the Lucy Collection at BUF and for allowing us to reclaim some of Dr. Lucy's specimens; and those people involved with helping us locate references to Dr. Lucy and the Elmira Academy of Sciences.

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# A NEW *SCHIEDEELLA* (ORCHIDACEAE: SPIRANTHINAE) FROM GUATEMALA[1]

DARIUSZ L. SZLACHETKO AND CHARLES J. SHEVIAK

ABSTRACT

*Schiedeella schlechteriana* Szlachetko & Sheviak is described as new. It is distinguished by a lip with narrowly rhombic hypochile and abruptly expanded epichile, dendritically proliferated nerves, and apically-directed auricles. It is compared with related species, one of which, *S. valerioi* (Ames & Schweinf.) Szlachetko & Sheviak, is formally transferred from *Spiranthes*.

Key Words: *Schiedeella,* new species, new combination, Guatemala

*Schiedeella* is a genus of Central American Spiranthinae characterized by nearly erect gynostemium; awl- or needle-like rostellum, with the rostellum remnant narrowly triangular and usually distinctly 3-dentate with the central tooth longest; nearly sheath-like viscidium; extremely reduced column foot; cuniculiform spur; basally nearly erect or only slightly arcuate lip; flat claw with unthickened margins; and herbaceous floral and cauline bracts. During a monographic study of the genus by the first author, three specimens constituting a single collection were found which are not referable to any recognized species and are here described as distinct:

**Schiedeella schlechteriana** Szlachetko & Sheviak, *sp. nov.*
(Figure 1)

Radices 3–4, tuberoso-incrassatae, 1.8–2.5 cm longae, 0.4–0.5 cm diametro, lanulosae. Caulis 6.5–8.0 cm altus, rectus, laevis, supra vaginam supremam glandulosus. Vaginae internodiis longiores, acutae, herbaceae, nervis parallelis paucis notatae. Folia tempore florendi fugacia. Inflorescentia 1.5–2.0 cm longa, 3–4 flora, laxa. Flores minuti, tubuliformes. Tepala ovario longiora. Labellum angustum, oblongum. Hypochilium 3 mm longum, 2.1 mm latum, basi duobus processibus carnosis ad apicem spectantibus instructum. Lobi laterales hypochilii triangulares. Isthmus (constrictio inter hypochilium et epichilium) gradatim angustatus.

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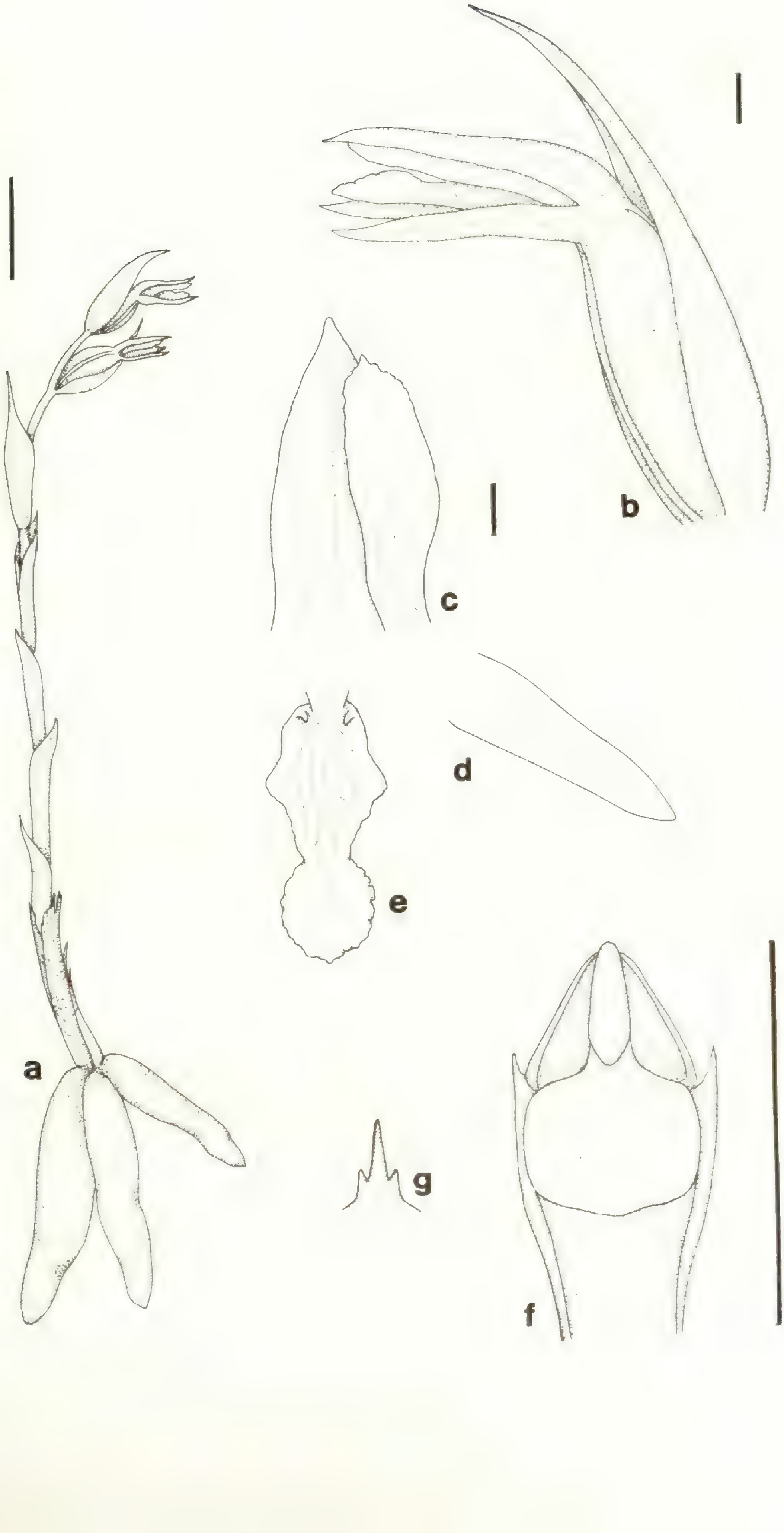
[1] Contribution #634 of the New York State Science Service.

Table 1. Characteristics of *Schiedeella schlechteriana* and similar species.

| Character | Expression | | | |
|---|---|---|---|---|
| | *S. schlechteriana* | *S. dendroneura* | *S. parasitica* | *S. valerioi* |
| Height (cm) | 6.5–8.0 | 10.0–20.0 | 11.0–40.0 | 14.0–43.0 |
| Root number | 3–4 | 1 | 1–4 | 1(–3) |
| Flower number | 2–3 | (3–)4–8(–9) | (2–)4–10(–20) | 3–6 |
| Length (mm) of: | | | | |
| Inflorescence | 15–20 | 25–50 | 30–100 | (30–)60–100(–130) |
| Floral Bract | 10 | 5–7 | 5–16 | 7–22 |
| Ovary | 5 | 5–6 | (3–)4–7(–9) | 4–11 |
| Dorsal Sepal | 5.2 | 5.0 | 4.5–7.1 | 4.3–7.2 |
| Lateral Sepal | 6.0 | 4.1 | 4.5–7.0 | 5.0–6.4 |
| Petal | 5.0 | 4.6 | 4.0–6.1 | 4.0–6.1 |
| Hypochile | 3.0 | 2.9 | 3.2–5.7 | 3.5–4.5 |
| Epichile | 2.0 | 1.6 | 1.4–3.0 | 1.0–1.7 |
| Gynostemium | 2.0 | 2.0 | 3.5–5.0 | 4.0–5.0 |
| Width (mm) of: | | | | |
| Dorsal Sepal | 1.3 | 1.8 | 1.2–2.5 | 1.1–2.0 |
| Lateral Sepal | 1.5 | 1.1 | 1.0–2.0 | 1.0–1.6 |
| Petal | 1.2 | 1.1 | 0.7–1.2 | 0.8–1.5 |
| Hypochile | 2.1 | 3.0 | 1.9–4.0 | 1.6–2.1 |
| Epichile | 2.0 | 2.1 | 2.0–3.0 | 1.0–1.9 |
| Lip division into hypo- & epichile | distinct | indistinct | distinct | indistinct |
| Auricles | antrorse | indistinct | cushion-like | indistinct |
| Red Callus | absent | absent | distinct | absent |
| Lip Venation | dendritic | dendritic | unbranched | unbranched |
| Glands on . . . | axis & sparsely on ovary | eglandular | axis, ovary, & bases of sepals | axis, sparsely sepals & ovary |

→

Figure 1. *Schiedeella schlechteriana*. Drawings from the Holotype (*Smith 559*: F). **a**: Plant; scale equals 1 cm. **b**: Flower and floral bract, lateral view; scale equals 1 mm. **c**: Dorsal sepal and petal, showing natural association; scale equals 1 mm. **d**: Lateral sepal; scale as in c. **e**: Lip, scale as in c. **f**: Gynostemium, ventral view, scale equals 1 mm. **g**: Rostellum remnant; scale as in f.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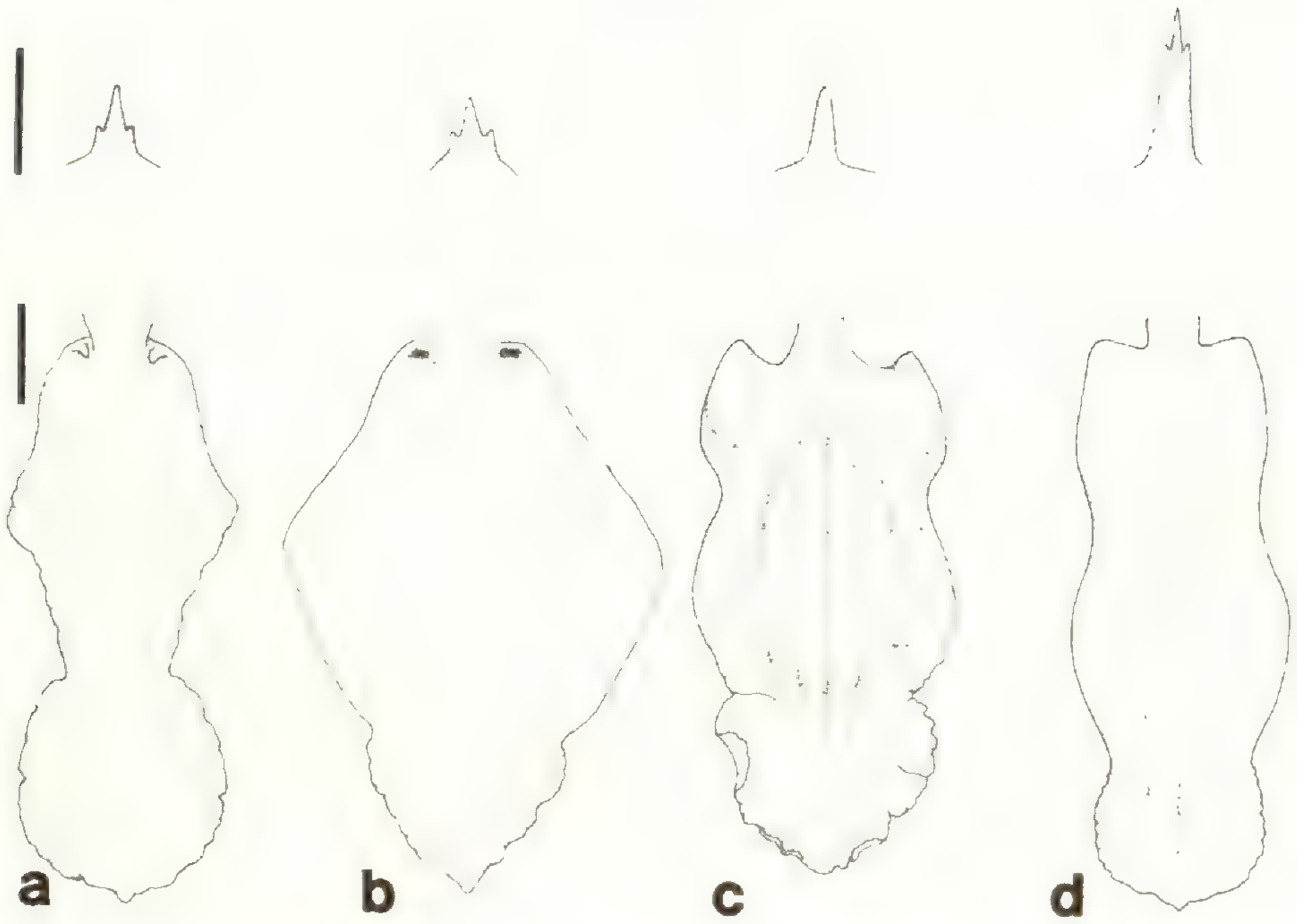


Figure 2. Rostellum remnants (above) and lips (below) of the four *Schiedeella* species discussed in the text. Scales equal 1 mm. **a**: *S. schlechteriana* Szlachetko & Sheviak. *Smith 559* (F) (HOLOTYPE). **b**: *S. dendroneura* (Sheviak & Bye) Burns-Balogh. *Bye 3944* (NYS) (HOLOTYPE). **c**: *S. parasitica* (Rich. & Gal.) Schltr. *Hagsater 6004* (AMO). **d**: *S. valerioi* (Ames & Schweinf.) Szlachetko & Sheviak. *Skutch 283* (US).

Epichilium 2 mm × 2 mm, plus minusve ovale, obtusum. Labelli incrassatio rubra absens, nervi dendroidei. Tepala cetera acuta, extus laevia. Gynostemium generi characteristicum. Rostellum viscidio ablato subulatum, latere utroque denticulo parvo instructum. Ovarium laxe glandulosum. Bracteae ovario circa duplo longiores herbaceae, 3 nervis ramificatis instructae.

Plants tiny. Roots 3–4, 1.8–2.5 cm long, 0.4–0.5 cm in diameter, tuberously thickened, lanulose. Stem 6.5–8.0 cm tall, erect, glabrous below, glandular above the uppermost bracts. Cauline bracts longer than the internodes (the uppermost reaching the inflorescence), sharply pointed, herbaceous, with parallel veins. Leaves basal, fugaceous, otherwise unknown. Inflorescence 1.5–2.0 cm long, laxly 2- or 3-flowered, the axis glandular. Flowers small, tubular. Perianth segments longer than ovary. Lip lacking a red callus, rather narrow, oblong, with distinctly dendritic proliferation of nerves. Hypochile 3 mm long, 2.1 mm wide, at the base the upper surface glandular with two fleshy, very small auricles bent toward the apex of the lip. Hypochile gradually tapered to

epichile, more or less rhombic, the side lobes triangular. Epichile 2 × 2 mm, oval, obtuse, the margin very minutely but distinctly erose. Dorsal sepal 6 mm long, 1.5 mm wide, lanceolate, indistinctly 3-nerved, glabrous. Lateral sepals 5.2 mm long, 1.3 mm wide, narrowly triangular, 1-nerved, glabrous. Petals 5 mm long, 1.2 mm wide, indistinctly falcate-banded, very thin, relatively broad, the apical margin erose, 3-nerved. Gynostemium very short. Rostellum remnant distinctly 3-dentate, the central tooth longer than the laterals. Viscidium nearly sheath-like. Ovary up to 5 mm long, sparsely glandular. Floral bracts 10 mm long, about twice as long as the ovary, thin, herbaceous, semi-translucent, acuminate, with 3 branched nerves.

TYPUS: GUATEMALA: Totonicapán: Totonicapán, Empuxet: En pastizal sobrepastoreado (*Agrostis exserta–Geranium alpicola*); exposición suroeste; pendiente moderado; plena sol. Perenne; flores blancas, el labio con marcaciones oxidas. Localmente común. 3200 m. 2 abr 1977. *D. N. Smith 559* (HOLOTYPE: F 1858096).

Known only from the type collection.

ETYMOLOGY: Named in honor of Rudolf Schlechter, who pioneered the revision of the Spiranthinae.

*Schiedeella schlechteriana* differs from any previously described species in the shape of the lip, apically-directed fleshy basal auricles on the lip, and by its diminutive nature, with very short, few-flowered inflorescences. It is most similar to three other species: *S. parasitica* (Rich. & Gal.) Schltr., *S. dendroneura* (Sheviak & Bye) Burns-Balogh, and *S. valerioi* (Ames & Schweinf.) Szlachetko & Sheviak. From *S. parasitica* it differs in the absence of a red callus on the lip, the venation of the lip, and the length of the gynostemium. From *S. valerioi* it differs in the type of venation, the distinct isthmus dividing the lip into evident epi- and hypochile, and in the length of the gynostemium. From *S. dendroneura* it differs in the presence of a distinct isthmus, glandular ovary and axis, and number of tuberous roots. These and other characteristics of the four species are compared in detail in Table 1 and illustrated in Figure 2.

During the course of this study it became apparent that *Schiedeella valerioi* should be maintained as distinct at the specific level, but that it had not in record been transferred to *Schiedeella* from *Spiranthes*. We do so here:

**Schiedeella valerioi** (Ames & Schweinf.) Szlachetko & Sheviak, *comb. nov.*

BASIONYM: *Spiranthes valerioi* Ames & Schweinf., Schedulae Orchidianae 10:8. 1930.

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# DISJUNCT POPULATIONS OF THE ALLEGED SERPENTINE ENDEMIC, *ASTER DEPAUPERATUS* (PORTER) FERN., ON DIABASE GLADES IN NORTH CAROLINA

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## ABSTRACT

A disjunctive range extension of the rare *Aster depauperatus* (Porter) Fern. is reported for the first time from several diabase glades in north central North Carolina. The species was previously known only from serpentine soils and the North Carolina populations hence represent an extension in both range and habitat.

Key Words: *Aster depauperatus*, diabase, serpentine, Granville Co., N. Carolina

The unusual properties of serpentine, notably a low calcium-to-magnesium ratio and relatively high concentrations of heavy metals, are linked with edaphic endemics wherever large bodies of serpentine occur (Brooks, 1987). The largest bodies of serpentine in the eastern United States form a narrow belt in the piedmont of Maryland and eastern Pennsylvania; these areas support a few endemic taxa (Reed, 1986; Brooks, 1987). Other serpentine outcrops occur in western North Carolina where the floristics and vegetation have been investigated by Radford (1948) and Mansburg and Wentworth (1984). These western North Carolina areas support a few disjuncts from the midwestern prairie regions, some of which also occur in Maryland and Pennsylvania, but none of the eastern United States endemics has been previously reported from these montane sites.

This note reports the occurrence of *Aster depauperatus* (Porter) Fern., one of the eastern North America serpentine endemics, from three diabase glades in Granville County in north central North Carolina. The previously known distribution of *A. depauperatus* coincides with that of serpentine barrens in Maryland, Pennsylvania (Wherry et al., 1979), and West Virginia (Reed, 1986). Reed (1986), however, cited a specimen from Nelson County, Virginia but *A. depauperatus* is not included in the recent *Atlas of Virginia Plants* (Harvill et al., 1986). Two of the newly

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discovered populations reported here are located within 1 km of each other and the third (at a locality described by LeGrand, 1988) is approximately 5 km distant from the first two. However, these sites are all part of one massive diabase intrusion (North Carolina Department of Natural Resources and Community Development, 1985). At all three sites *A. depauperatus* is a very common and conspicuous member of the fall flora with populations of well over 100 plants at each locality.

The vegetation of the diabase glades occurs on a substrate of Iredell soil which can be recognized by small surficial iron concretions to 1 cm diameter and a subsurface clay hardpan (Batson, 1952, Ph.D. thesis, Duke University, Durham, NC). The circumneutral pH of these sites contrasts with the surrounding acidic soils bordering the diabase intrusion. Floristically, the diabase glades harbor a mixture of species from habitats of high endemism in the eastern United States; representatives from granitic outcrops include *Portulaca smallii* P. Wilson, *Crotonopsis elliptica* Willd., and *Cyperus granitophilus* McVaugh (McVaugh, 1943); species most often associated with limestone cedar glades in Tennessee and Missouri include *Isanthus brachiatus* (L.) BSP., *Scutellaria parvula* Michx., *Berberis canadensis* P. Mill., *Silphium terebinthinaceum* Jacq., and the rhizomatous *Parthenium hispidum* Raf. (Steyermark, 1963). Moreover, in addition to *Aster depauperatus,* these glades also support *Polygonum tenue* Michx., a characteristic member of serpentine barrens (Wherry, 1963; Reed, 1986). Other species, of note because of their sporadic occurrence in piedmont North Carolina, include *Solidago rigida* L., *Eupatorium altissimum* L. (= *Ageratina altissimum* (L.) Spach), *Lotus helleri* Britt., and *Paronychia fastigata* (Raf.) Fern.

Our identification of the *Aster* was based upon morphological comparisons of the North Carolina plants with herbarium specimens (DUKE, PA, PH) as well as with measurements given in Hart (1980) and Fernald (1970). Several plants from each locality were transplanted and grown in the greenhouse to determine if the characteristic morphology is retained under less restrictive conditions. Chromosome counts were conducted to confirm the morphological determinations.

In *Aster depauperatus* the basal and lower cauline leaves are lost prior to anthesis, and new basal leaves emerge near the end of the flowering season. Because most herbarium specimens are of flowering material, there are either no basal leaves or they are

Table 1. Comparison of morphological characters of *Aster depauperatus* between Maryland and Pennsylvania serpentine barrens and North Carolina diabase glades. For Maryland–Pennsylvania plants, number of disk florets is from Fernald (1950) and basal leaf measurements are from Hart (1980); for North Carolina plants, basal leaf measurements are from greenhouse-grown plants; all other values are from herbarium specimens. All values are in cm $\bar{x}$ = mean, SD = standard deviation.

| | | Character | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | No. Disk Florets | Capitula | | Basal Leaf | | Cauline Leaf | |
| | | | Length | Width | Length | Width | Length | Width |
| Serpentine (MD–PA): | $\bar{x}$ | 6–12 | 0.43 | 0.44 | 6.10 | 0.59 | 2.82 | 0.14 |
| | SD | — | 0.04 | 0.05 | 0.80 | 0.05 | 0.78 | 0.05 |
| Diabase (NC): | $\bar{x}$ | 8.30 | 0.41 | 0.41 | 4.26 | 0.73 | 2.20 | 0.12 |
| | SD | 1.60 | 0.03 | 0.06 | 0.79 | 0.07 | 1.21 | 0.04 |

immature. For these reasons we compared basal leaf measurements of our greenhouse-grown plants to those of common garden plants of *A. depauperatus* cited in Hart (1980).

The North Carolina plants were indistinguishable from *Aster depauperatus* on the basis of basal and cauline leaf widths, capitula sizes, involucral features of bract shape and texture, the number of disk florets per head, and the deciduous nature of basal and lower cauline leaves (Table 1). These distinctive traits were retained in greenhouse-grown plants and therefore we conclude that the North Carolina populations represent a disjunct series of populations of *A. depauperatus* where the plants inhabit a newly-recorded substrate for the species.

Chromosome numbers in four plants were counted to confirm our initial morphological determination. Mitotic chromosomes in root tips of plants that had been transplanted into the greenhouse were stained with aceto-carmine. The diploid chromosome number in all four plants was $2n = 16$. Two previous reports of the chromosome number in *Aster depauperatus,* both on plants from the serpentine barrens in Pennsylvania, also found $2n = 16$ (Morton, 1981; Semple and Chmielewski, 1985). In *A. pilosus,* chromosome numbers throughout the range of the species were between $2n = 32$ and $2n = 48$ (one count of $2n = 56$) (Semple and Chmielewski, 1985). Thus, cytologically in addition to morphologically, the plants in Granville County are similar to those on serpentine barrens to the north.

Curiously, there are some outcroppings of serpentine in adjacent Wake County, North Carolina (Dickey, 1963, M.S. thesis, North Carolina State University, Raleigh, NC) but at these sites neither *Aster depauperatus* nor any of the above-mentioned associated species was seen. These small serpentine intrusions do support a stunted open canopy, however, dominated by *Pinus echinata* P. Mill. and *Quercus marilandica* Muenchh. with *Andropogon scoparius* Michx. and *Stipa avenacea* L. in the understory. Furthermore, *Aster depauperatus* was not found on similar diabase sites in neighboring Durham County or even in nearby sites in Granville County; it is seemingly restricted to only a few localized populations.

North Carolina Specimens Examined. Granville Co.: Butner diabase glade, E side of Route 1100 about 1.5 mi. N of railroad tracks crossing 1100, *Levy s.n.* 8 X 1987 (DUKE); 1.5 mi. S of Butner Route 1103 on 1209, *Levy s.n.* 15 VIII 1988 (DUKE); on Iredell soil about 1 mi. W of Butner along Interstate 85, *Levy s.n.* 7 IX 1988 (DUKE); diabasic heavy clay soils about 2.5 mi. SE of Butner on County Rd. 1209 paralleling U.S. Interstate 85, *Wilbur 44700 A, 44703* (DUKE); diabasic soils about 2 mi. SE of Butner on State Rd. 1209 paralleling Interstate 85, *Wilbur 44676* (DUKE); *RLW 51709* (DUKE, GA, GH, NCU, NY, PA, PH, US, USCH); heavy clay soils about 2 mi. E of Butner on State Rd. 1209 paralleling Interstate 85 about 1 mi. from its intersection with SR 1103 at site being rapidly destroyed by off-road vehicles, *Wilbur 51690* (DUKE); forest glade 2 mi. N of Butner on State Rd. 1100 on diabasic soil, *Wilbur 51674, 51675* (DUKE).

Although the occurrence of *Aster depauperatus* in the diabase glades is of biogeographic interest, it is not wholly anomalous. Iredell soils in Granville County possess a higher pH relative to adjacent soil types (6.4 versus 5.0 respectively) (Dayton, 1966). Possibly of greater importance to the establishment and persistence of serpentine endemics are the calcium and magnesium concentrations. Although these Iredell soils have a much higher calcium content compared to typical serpentine soils (7–10 mEq/100 g versus 0.2–4.0 mEq/100 g), the Iredell soils are also quite high in exchangeable magnesium relative to adjacent soils (5–7 mEq/100 g versus 0.1–0.3 mEq/100 g) (Dayton, 1966; Proctor and Woodell, 1975). There is evidence that some serpentine endemics require high absolute levels of magnesium (Proctor and Woodell, 1975). Thus, the diabasic glades, newly reported as habitats for *Aster depauperatus,* contain some but not all of the characteristics of serpentine barrens.

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# RARE PLANTS IN COASTAL HEATHLANDS: OBSERVATIONS ON *COREMA CONRADII* (EMPETRACEAE) AND *HELIANTHEMUM DUMOSUM* (CISTACEAE)

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**ABSTRACT**

The effects of prescribed burning experiments on two rare coastal heathland species are described. Fire killed adult *Corema conradii* Torr., but resulted in abundant seedling regeneration. Ants may be important vectors in the dispersal of *Corema* fruits. Following a spring burn, both cover and flowering of *Helianthemum dumosum* (Bickn.) Fern. increased. Seedlings of this species also were more common, especially where cover of *Cladonia* lichens was reduced. Occasional fire may be necessary to maintain healthy, reproductive populations of these species.

Key Words: *Corema conradii, Helianthemum dumosum,* heathlands, fire ecology, myrmecochory, Nantucket

Coastal heathlands are found from New Jersey to the Canadian maritime provinces. This vegetation type is dominated by low shrubs primarily in the Ericaceae, but also includes heath-like members of the Empetraceae, Myricaceae, and Cistaceae (Harshberger, 1914; Tiffney and Eveleigh, 1985). However, because of increasing losses resulting from plant succession and real estate development, coastal heathlands are now considered threatened throughout their range. As part of the Massachusetts Audubon Society's long-term studies on the origin, dynamics, and management of coastal heathlands in New England (Dunwiddie and Caljouw, 1989; Dunwiddie, 1989) prescribed burns have been carried out since 1983 to examine the effects of fire on this community. I describe here observations on two heathland species of "special concern" (as defined by the Massachusetts Natural Heritage Program, Sorrie, 1987) made in connection with these studies on Nantucket Island.

*Corema conradii* Torr., Broom Crowberry, is a low-growing, dioecious, evergreen shrub, seldom exceeding 30 cm in height. Both male and female flowers are inconspicuous, and are apparently wind pollinated. On Nantucket, the species is usually the first of the native taxa to flower, reaching anthesis by mid- to late

March. I have recorded flowering as early as January; most plants have finished blooming by May.

The spherical fruits ripen by July, average 1 mm in diameter, and have been described as dry, juiceless drupes with 3 (4–5) nutlets (Gray, 1848; Fernald, 1950). However, on many specimens, I observed that the basal portion of these fruits develops into a white, fleshy structure that occasionally exceeds the size of the remainder of the fruit. I can find no description in the literature of this structure, which remains fleshy for several weeks, and appears to function much like an elaiosome on a seed. Ants in the complex *Aphaenogaster rudis* were observed collecting these fruits and returning with them to their burrows. Fruits with the fleshy basal portion eaten off were carried out of the burrows, and dropped in mounds in front of the burrows; one such mound had approximately 3700 fruits in it. There was no evidence of damage to the nutlets within the fruits, and studies are continuing to determine the role of myrmecochory in the regeneration of Broom Crowberry.

On Nantucket, *Corema conradii* occasionally occurs in dense patches covering several hectares. These patches are reminiscent of European *Calluna* and *Erica* heathlands, where senescent individuals gradually die out in the center, leaving bare patches in which lichens and other species may appear. Ages of the oldest individuals of *Corema*, determined by counting annual branching nodes, exceeded 40 years. Concerns regarding the virtual absence of *Corema* seedlings in these aged patches led to the experiment described here, in which a 20 × 20 m square plot within one such patch was burned on 12 April, 1987. The occurrence of *C. conradii* in areas with high fire frequencies, such as the pine barren plains of New Jersey (Good et al., 1979), suggested that it might be well adapted to fire, although Stone (1911) reported its extermination by severe fire.

A total of thirteen vascular plants was recorded within the plot prior to burning, but data from thirty vegetation quadrats (20 × 100 cm) emphasized the extremely low diversity of this vegetation. Only three species had cover values that exceeded 1%: *Corema* (61%), *Arctostaphylos uva-ursi* (L.) Sprengel (21%), and *Cladonia* spp. (43%). Both headfires and backfires were used to burn the plot, although no differences were detected in terms of impacts on plants or soil humus. Virtually all above-ground portions of

plants in the plot (except *Quercus ilicifolia* Wang. and *Pinus rigida* Miller) were consumed by the burn, but the layer of humus 2–4 cm thick, comprised primarily of *Corema* leaves, remained moist and largely undisturbed.

All of the *Corema* was killed by the fire, and no seedlings were observed during the first summer, despite an abundant seed bank visible in and on the soil. Other species, all perennial plants present within the plot prior to the burn, were observed resprouting, although no seedlings were noted in July. At the end of the first year (1987), *Arctostaphylos* had returned to half (11%) of its original cover.

In June of 1988, seedlings of several species were noted, primarily *Corema, Arctostaphylos,* and *Hudsonia ericoides* L.; counts in thirty-eight 0.25 $m^2$ quadrats yielded a total of 383, 42, and 22 individuals, respectively. The *Corema* seedlings were so large (up to 1 cm tall) that I suspected they had germinated the previous fall. Subsequent observations in October, 1988, revealed a new crop of germinating seedlings, suggesting that the original crop also may have sprouted in the fall following the burn. Studies are continuing to determine growth rates, recruitment, and mortality in this new *Corema* population. Initial observations indicate that individuals may be growing more vigorously when associated with an *Arctostaphylos* nurse plant. However, *Arctostaphylos* had reached 33% cover at the end of 1988, exceeding its pre-burn levels, and it is likely to dominate this area for some time.

*Helianthemum dumosum* (Bickn.) Fern., Bushy Rockrose, is endemic to southern New England, and occurs frequently on Nantucket in the more diverse and herbaceous-rich coastal heathlands, sometimes referred to as sandplain grasslands. This perennial herb, up to 25 cm tall, has perfect flowers with bright yellow petals in early summer, but produces only cleistogamous flowers later in the season.

In order to determine the effects of fire on *Helianthemum,* a two-hectare burn was conducted on April 1, 1988 that included a large population of bushy rockrose. Measurements were made to determine changes in three parameters thought to be potentially affected by burning: plant cover, flowering, and seedling establishment. These variables were measured in thirty 0.25 $m^2$ quadrats arranged along three 10 m long transects in the area to be burned, and on two other transects in a nearby control area. Each quadrat was subdivided into one hundred 5 cm squares, and data were collected on the presence of seedlings, flowers, and adult

Table 1. Data on *Helianthemum* from burned and control plots before (1987) and after (1988) treatment. All data are reported as average number of occurrences per 0.25 $m^2$ quadrat (see text).

| | | Adults | Flowers | Seedlings |
|---|---|---|---|---|
| Treatment: | 1987 | 34.3 | 6.7 | 1.5 |
| | 1988 | 47.2 | 23.0 | 3.2 |
| Control: | 1987 | 15.3 | 3.8 | 2.3 |
| | 1988 | 15.7 | 4.4 | 2.4 |

*Helianthemum* plants in each square. The data are therefore constrained to values from 0–100. This method was adopted because the bushy growth form and dense vegetation made it difficult to distinguish individual plants. Data were gathered in June, 1987, and again in June, 1988, following the burn, and are summarized in Table 1.

Changes in the vigor of adult *Helianthemum* plants resulting from burning were assessed by examining changes in the number of squares containing adult plants in each quadrat. This value (Table 1) increased in 1988 by about 40% over the 1987 values in the burned plot, whereas the control plot remained unchanged. Flowering showed an even greater change, increasing by nearly a factor of four after burning. Seedlings were also twice as abundant as before.

Aspects of *Helianthemum dumosum* seedling establishment in other burned areas on Nantucket are also worth noting. At one site, lichens (*Cladonia* spp.) averaged 20–40% cover, in many places blanketing essentially all of the ground surface not occupied by bunch grasses and other vascular plants. *Helianthemum* seedlings were extremely rare in these areas prior to burning. After a March burn, however, lichen cover dropped to <2%, and numerous *Helianthemum* seedlings sprouted in the bare openings. Because the lichens are so slow to re-establish, it appears likely that many of these seedlings will survive. These results and observations suggest that both lichens and dense litter cover may inhibit seedling establishment of *Helianthemum.*

The studies described here indicate an important potential role of fire in the population dynamics of two coastal heathland species. Although adult *Corema* plants may be killed by fire, significant reproduction may only occur following such events. Maintenance of viable populations of individuals of different ages may require a management regime spanning many decades, in which small patches within each population are occasionally burned, but large

areas are left alone. Growth of adult *Helianthemum* plants appears to be enhanced by fire, which also encourages its regeneration. Additional studies are needed to determine the effects of repeated fires on growth and mortality of both these species.

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# ENDANGERED PLANTS OF FAKAHATCHEE STRAND STATE PRESERVE

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## ABSTRACT

Analysis of the plants in the Fakahatchee Strand State Preserve shows that large numbers of them are on one or more of the rare plant lists. Twenty-seven families and 106 species known from in or near the Preserve are either endangered, threatened and/or commercially exploited. Species endangered in some way constitute 22.2% of those known from the Preserve. This large number of endangered plants within the Preserve heavily reflects the abundant tropical epiphytic element within the temperate plant communities. Comparisons are made with other southern Florida areas to show the uniqueness of the Preserve flora.

Key Words: Endangered plants, Fakahatchee Strand State Preserve, Florida

## INTRODUCTION

Many people have been working with endangered plants of Florida for some years, yet few studies have specifically addressed the numbers and percentages of these actual species within designated areas. Most of the existing studies have been made on a species by species basis (e.g., Austin, 1977, 1979, 1981, 1983a, 1983b, 1984, 1986; Austin, Krauss and McMahon, 1978, "Rare and Endangered Plants of Southeastern Florida," report for Connell Metcalf and Eddy, Inc., Coral Gables; Austin and Alvarez, 1979, "Management of the Fakahatchee Strand State Preserve," report for Department of Natural Resources, Tallahassee, FL, and Joint Center for Environmental and Urban Problems, Florida Atlantic University, Boca Raton; Austin, Nauman and Tatje, 1980, "Endangered Species of Southern Florida," report for U.S. Fish and Wildlife Service, Office of Endangered Species, Atlanta, GA; Austin, Nauman and Krauss, 1981, "Endangered Species of Southern Florida," report for U.S. Fish and Wildlife Service, Office of Endangered Species, Atlanta, GA; Ward, 1979; inter alia).

With the current knowledge of the plants in the Fakahatchee Strand State Preserve (Austin et al., 1986, 1989), we know that the Preserve has 27 families and 106 species on one or more of the current endangered plant lists (Table 1). This number constitutes over one-fifth of the species (22.2%) known to exist within

or near the borders of the Preserve (Austin et al., 1989). Moreover, these species grow in a preserve that is about 32,640 hectares (80,640 acres), a small area compared to that of the nearby Big Cypress National Preserve.

Species on the endangered list in Fakahatchee Strand State Preserve include 13 families and 33 species of ferns and fern allies, and one cycad. Of these, one fern (*Thelypteris grandis*) has been found nowhere else in the United States (Nauman, 1979). Within the flowering plants there are 11 species of Bromeliaceae, 23 species of Orchidaceae, and four species of Piperaceae, a total of 38 epiphytic species. This epiphytic element constitutes 36% of the endangered flora. Moreover, there are several other orchids that are semi-epiphytic (e.g., *Liparis, Malaxis*). These numbers also include an orchid (*Maxillaria conferta*) that has not been found elsewhere within the United States. This number of epiphytes is probably unequaled elsewhere in Florida, and is nowhere exceeded. The balance of endangered species (10 families) within the Fakahatchee Strand State Preserve is made up of non-epiphytic herbs, shrubs and trees.

## DISCUSSION

The Fakahatchee Strand State Preserve flora may now be compared to other local floras because of the recent species list compilation. Lists for four parks and preserves are compared below (Austin et al., 1978, op. cit.; Duever et al., 1979; Avery and Loope, 1980; Black and Black, 1980).

Duever et al. (1979) made a study that addressed the number of endangered species in the adjacent Big Cypress National Preserve. Within its 230,769 hectares (570,000 acres), an area considerably larger than Fakahatchee Strand State Preserve, Duever et al. (1979) found 124 species considered rare and endangered; their list included occurrences not verified by them or by others. They also noted nine species as being listed by the Florida Department of Agriculture (FDA), which never have been included there (Wood, 1988). They additionally noted three species from the Florida Committee on Rare and Endangered Plants and Animals (FCREPA) list which have not been adopted by the Florida Game and Freshwater Fish Commission. Our corrected total of their endangered species on all lists is 113.

Since the publication by Duever et al. (1979), a more complete

checklist (Black and Black, 1980) has become available for Big Cypress National Preserve. This later list calls into question several of the earlier-included species. Of the 636 species Black and Black, 1980, were able to confirm in the Big Cypress National Preserve, only 81 (or 12.7%) are on the Endangered and Commercially Exploited species lists. If one includes their "possible" list, another 22 species may be added. This inclusion brings the total to 103 endangered species as possibly occurring in the Big Cypress National Preserve, and results in 16.2% of the total flora being endangered; it resolves many of the differences between these two reports. Furthermore, Black and Black, 1980, listed some 23 families which included their potential endangered species. No matter which list is used, the figures on endangered families and species are similar to those listed for Fakahatchee Strand State Preserve. However, the percentage of endangered flora is still well below the figure we found for Fakahatchee Strand State Preserve.

The Fakahatchee Strand State Preserve clearly has a flora similar to that of Big Cypress National Preserve, but in only about one-seventh the geographical area. A comparison of the uncorrected Duever et al. (1979) Big Cypress National Preserve list with the present one for Fakahatchee Strand State Preserve shows a 77.4% similarity (96 shared species of 124) in the flora considered endangered by Duever et al. (1979). A smaller percentage in the Big Cypress National Preserve (78 of the 124 species or 62.9%) is shared with Everglades National Park (Avery and Loope, 1980). Fakahatchee Strand State Preserve has almost twice as many endangered species as Big Cypress National Preserve (29 vs. 15), while Big Cypress National Preserve has more threatened species (95 vs. 65).

Austin et al. (1978, op. cit.) made a study for the area around the Turkey Point Power Plant farther east in Dade County. Their study used its own criteria for assigning endangerment, not those applied by Federal and by state agencies. These authors found 175 species in an eight-mile radius around the power plant which they considered to range from Rare to Endangered. Since the exact total flora of the area studied is not known, further comparisons are impossible. Most of the plants in this study are now either on the Florida Department of Agriculture (FDA) list, or were proposed for inclusion by the 1989 legislative session.

Study of the Key Deer and Great White Heron Refuges (Austin

Table 1. Species of endangered (*), threatened and commercially exploited plants in the Fakahatchee Strand State Preserve.

(*) Key to Abbreviations: **C** = Commercially Exploited; **E** = Endangered; **FDA** = Florida Department of Agriculture; **PC** = Proposed as Commercially Exploited by FDA for 1989 session; **PD** = Proposed for deletion by FDA for 1989 session; **PT** = Proposed as Threatened by FDA for 1989 session; **T** = Threatened; **UR1** = Under Review for federal listing, with substantial evidence for some degree of biological vulnerability and/or threat; **UR2** = Under Review for federal listing, but substantial evidence of biological vulnerability and/or threat is lacking; **UR4** = Still formally Under Review for listing, but no longer being considered for listing because current taxonomic understanding indicates species is an invalid taxon and thus ineligible for listing; **UR5** = Still formally Under Review for listing, but no longer considered for listing because recent information indicates species is more widespread or abundant than previously believed; **USFWS** = United States Fish and Wildlife Service.

## A. Ferns and Fern Allies

1. Aspidiaceae

*Ctenitis sloanei* (Poepp.) Morton—Florida tree fern. FDA: T.
*C. submarginalis* (Langsd. & Fisch.) Copel.—Comb fern. FDA: T.
*Thelypteris dentata* (Forsk.) E. P. St. John—Downy wood fern. FDA: T.
*T. grandis* A. R. Smith—Large wood fern. First recorded in Florida by Nauman (1979). FDA: T.
*T. hispidula* (Dcne.) Reed var. *versicolor* (E. P. St. John) A. R. Smith—Hispid marsh fern. FDA: T.
*T. interrupta* (Willd.) Iwatsuki—Marsh fern. FDA: T.
*T. kunthii* (Desv.) Morton—Downy marsh fern. FDA: T.
*T. palustris* Schott—Marsh fern. FDA: T.
*T. reticulata* (L.) Proctor—Reticulate marsh fern. FDA: T.

2. Aspleniaceae

*Asplenium auritum* Sw.—Eared spleenwort. FDA: E.
*A. serratum* L.—Birdnest fern. FDA: E.

3. Davalliaceae

*Nephrolepis* ×*averyi* Nauman—Avery's sword fern. FDA: T.
*N. biserrata* (Sw.) Schott—Giant sword fern. FDA: T.
*N. exaltata* (L.) Schott—Sword fern. FDA: T.

4. Isoetaceae

*Isoetes flaccida* Shuttlew. ex A. Braun—Quillwort. Found by Taylor Alexander (pers. comm.) just north of Alligator Alley (St. Rd. 84) in the Big Cypress. Probably also occurs south of this road in Fakahatchee. FDA: T.

5. Lycopodiaceae

*Lycopodium dichotomum* Jacq.—Hanging clubmoss. FDA: E.

6. Ophioglossaceae

*Ophioglossum palmatum* L.—Hand fern. FDA: E.
*O. petiolatum* (L.) Mett.—Adder's tongue fern. FDA: T.

7. Osmundaceae

*Osmunda cinnamomea* L.—Cinnamon fern. FDA: PT, PC.
*O. regalis* var. *spectabilis* (Willd.) Gray—Royal fern. FDA: C.

Table 1. Continued.

8. Polypodiaceae
*Campyloneurum angustifolium* (Sw.) Fée—Narrow strap fern. FDA: E.
*C. costatum* (Kuntze) K. Presl—Tailed strap fern. FDA: E.
*C. phyllitidis* (L.) Presl f.—Strap fern. FDA: T.
*C. phyllitidis* f. *latum* (Moore) Proctor—Stalked strap fern. FDA: T.
*Phlebodium aureum* (L.) J. E. Smith—Cabbage palm fern. FDA: T.
*Polypodium ptilodon* var. *caespitosum* (Jenman) A. M. Evans—Greater comb fern. FDA: T.
9. Psilotaceae
*Psilotum nudum* (L.) Pal.-Beauv.—Whisk fern. FDA: T.
10. Pteridaceae
*Acrostichum aureum* L.—Coastal leather fern. FDA: E.
*A. danaeifolium* Langsd. & Fisch.—Leather fern. FDA: T.
*Pteris vittata* L.—Ladder brake. FDA: T.
*P. tripartita* Sw.—Giant brake. Widespread, although sporadic. Not confirmed within the Preserve. FDA: T.
11. Salviniaceae
*Azolla caroliniana* Willd.—Mosquito fern. FDA: T, PD.
12. Vittariaceae
*Vittaria lineata* (L.) J. E. Smith—Shoe-string fern. FDA: T.

**B. Cycads**

13. Cycadaceae
*Zamia pumila* L.—Coontie. Oral report by Ranger Goble from the northwestern pine islands in the Preserve, but not confirmed. FDA: C.

**C. Flowering Plants**

14. Acanthaceae
*Elytraria carolinensis* (J. F. Gmel.) Pers. var. *angustifolia* (Fernald) Blake. FDA: T.
15. Aquifoliaceae
*Ilex cassine* L.—Dahoon holly. FDA: PC.
16. Arecaceae
*Acoelorraphe wrightii* (Griseb. & Wendl.) Wendl. ex Becc.—Paurotis palm. FDA: T.
*Roystonea elata* (Bartr.) Harper—Royal palm. FDA, USFWS: E, UR1.
17. Asteraceae
*Melanthera parvifolia* Small (= *Melanthera nivea* (L.) Small). USFWS: UR2.
18. Bromeliaceae
*Catopsis berteroniana* (Schultes f.) Mez—Yellow catopsis. FDA: E.
*C. floribunda* (Brongn.) L. B. Smith—Many-flowered catopsis. FDA: E.
*C. nutans* (Sw.) Griseb.—Small catopsis. FDA: E.
*Guzmania monostachia* (L.) Rusby ex Mez—Strap-leaved air plant. FDA: E.
*Tillandsia balbisiana* Schultes—Reflexed wild pine. FDA: T.
*T. fasciculata* Sw.—Stiff-leaved wild pine. FDA: C.
*T. paucifolia* Baker (= *T. circinnata* Schlecht.)—Twisted wild pine. FDA: T.

Table 1. Continued.

*T. pruinosa* Sw.—Fuzzy-wuzzy air plant. FDA: E.
*T. setacea* Sw.—Needle-leaf air plant. FDA: T.
*T. utriculata* L.—Giant wild pine. FDA: C.
*T. variabilis* Schlecht. (= *T. valenzuelana* A. Richard)—Soft-leaved wild pine. FDA: T.

19. Burmanniaceae
*Burmannia flava* Mart.—Fakahatchee burmannia. FDA: E.
20. Euphorbiaceae
*Stillingia sylvatica* ssp. *tenuis* (Small) Rogers—Corkwood. USFWS: UR2.
21. Lentibulariaceae
*Pinguicula pumila* Michx.—Butterwort. FDA: PT.
*Pinguicula* sp.—Butterwort. Different from the preceding fide A. Herndon. Specimen not seen. FDA: PT.
22. Myrtaceae
*Myrcianthes fragrans* (Sw.) McVaugh var. *simpsonii* (Small) Long—Simpson's stopper. USFWS: UR2.
23. Orchidaceae
*Bletia purpurea* (Lam.) DC.—Pine pink. FDA: T.
*Bulbophyllum pachyrhachis* (A. Richard) Griseb.—Rat-tail orchid. FDA: E.
*Calopogon pallidus* Chapman—Pale grass-pink. FDA: T.
*C. tuberosus* (L.) BSP.—Grass pink. FDA: T.
*Campylocentrum pachyrrhizum* (Reichenb. f.) Rolfe—Crooked-spur orchid. FDA: E.
*Cyrtopodium punctatum* (L.) Lindley—Cow-horn orchid. FDA: E.
*Encyclia cochleata* (L.) Dressler (= *Anacheilum cochleatum* (L.) Hoffmannsegg)—Clam-shell orchid. FDA: T.
*E. pygmaea* (Hook.) Dressler—Dwarf epidendrum. FDA: E.
*E. tampensis* (Lindley) Small—Butterfly orchid. FDA: T.
*Epidendrum anceps* Jacq.—Brown orchid. FDA: T.
*E. blancheanum* Urban (= *E. acunae* Dressler)—Ramose orchid. FDA: E.
*E. difforme* Jacq. (= *Neolehmannia difformis* (Jacq.) Pabst)—Umbelled orchid. FDA: T.
*E. nocturnum* Jacq.—Night orchid. FDA: T.
*E. rigidum* Jacq.—Rigid orchid. FDA: T.
*E. strobiliferum* Reichenb. f.—Twisted orchid. FDA: T.
*Erythrodes querceticola* (Lindley) Ames (= *Platytheles querceticola* (Lindley) Garay—Oak orchid. FDA: T.
*Eulophia alta* (L.) Fawcett & Rendle—Wild coco. FDA: T.
*Habenaria distans* Griseb.—False water-spider orchid. FDA: T.
*H. nivea* (Nutt.) Sprengel (= *Platanthera nivea* (Nutt.) Luer)—Snowy orchid. FDA: T.
*H. odontopetala* (Reichenb.) Small—Tooth-petal orchid. Doubtful (based on oral report); no specimen known. FDA: T.
*H. quinqueseta* (Michx.) A. A. Eaton—Long-horned orchid. FDA: T.
*H. repens* Nutt.—Water spider orchid. FDA: T.
*Harrisella filiformis* (Sw.) Cogn. (= *H. porrecta* (Reichenb.) Fawcett & Rendle)—Extended orchid. FDA: T.

Table 1. Continued.

*Ionopsis utricularioides* Lindley—Delicate orchid. FDA: E.
*Leochilus labiatus* (Sw.) Kuntze—Smooth lip orchid. Doubtful (based on oral report); no specimen known. FDA: T.
*Lepanthopsis melanantha* (Reichenb. f.) Ames—Tiny orchid. FDA: E.
*Liparis nervosa* (Thunb.) Lindley (= *L. elata* Lindley)—Shiny-leaf orchid. FDA: T.
*Malaxis spicata* Sw.—Florida malaxis. FDA: T.
*Maxillaria crassifolia* (Lindley) Reichenb. f.—False butterfly orchid. FDA: E.
*M. conferta* (Griseb.) C. Schweinf. ex Leon—Originally found by Roger Hammer, and later reported by him for Collier Co. (Bull. Fairchild Trop. Gard. 36: 16–18. 1981). A specimen was collected by Carl Luer; there is a voucher at the Marie Selby Botanical Gardens (SEL), Sarasota (R. M. Adams, pers. comm.). FDA: T.
*Oncidium floridanum* Ames—Mule-ear orchid. FDA: T.
*Pleurothallis gelida* Lindley—Frosted-flower orchid. FDA: T.
*Polyrrhiza lindenii* (Lindley) Cogn.—Ghost orchid. FDA: E.
*Polystacha concreta* (Jacq.) Garay & Sweet—Many-spiked orchid. FDA: T.
*Ponthieva racemosa* (Walt.) Mohr—Shadow witch. FDA: T.
*Spiranthes cernua* (L.) L. C. Rich. var. *odorata* (Nutt.) Correll—Nodding ladies' tresses. FDA: T.
*S. cranichoides* (Griseb.) Cogn. (= *Beadlea cranichoides* (Griseb.) Small)—Helmit ladies' tresses. FDA: T.
*S. lacinata* (Small) Ames—Lace-lip ladies' tresses. FDA: T.
*S. lanceolata* (Aublet) Leon var. *lanceolata* (= *Stenorrhynchos lanceolatus* (Aublet) L. C. Rich ex Spr.; *Sacoila lanceolata* (Aubl.) Garay). FDA: T.
*S. lanceolata* var. *paludicola* Luer (= *Sacoila lanceolata* var. *paludicola* (Luer) Sauleda et al.)—Fakahatchee ladies' tresses. FDA, USFWS: T, UR2.
*S. longilabris* Lindley—Long-lip ladies' tresses. FDA: T.
*S. praecox* (Walt.) Watson—Giant ladies' tresses. FDA: T.
*S. vernalis* Engelm. & Gray—Spring ladies' tresses. FDA: T.
*Vanilla phaeantha* Reichenb. f.—Leafy vanilla. FDA: T.

24. Piperaceae

*Peperomia glabella* (Sw.) A. Dietr.—Cypress peperomia. FDA: E.
*P. humilis* A. Dietr. For reasons that are not clear, Avery and Loope (1981) reported this species under the name *P. questeliana* Stehel & Trel. This name is clearly a later one since it was published in 1940 and *P. humilis* was published in 1831. *See* Boufford, J. Arnold Arbor. 63: 324. 1982. FDA: E.
*P. obtusifolia* (L.) A. Dietr. (= *P. floridana* Small)—Florida peperomia. FDA: E.
*P. simplex* Ham.—Green peperomia. Reported by Long and Lakela (1971); no specimen seen. *See* Boufford, J. Arnold Arbor. 63: 324. 1982. FDA: E.

25. Poaceae

*Schizachyrium scoparium* (Michx.) Nash [= *S. rhizomatum* (Swallen) Gould]—Little bluestem. FDA, USFWS: E, UR4.

Table 1. Continued.

| | |
|---|---|
| 26. Rhamnaceae | |
| *Sageretia minutiflora* (Michx.) Mohr—Buckthorn. | USFWS: UR5. |
| 27. Sapotaceae | |
| *Chrysophyllum oliviforme* L.—Satinleaf. | FDA: E. |

et al., 1980, op. cit.) showed that they supported 94 families and 492 species. Of this total, only 19 families and 41 species (8.3%) are endangered. These figures include seven families and 14 species of ferns, as well as six Bromeliaceae, and one Orchidaceae.

All data indicate that Fakahatchee Strand State Preserve has a higher percentage of endangered species than other southern Florida parks and preserves. Moreover, all these data reinforce the contention that has been voiced over the past decade and a half that southern Florida has more endangered species than most other areas in the eastern United States. Of the 282 species listed in one category or another for southern Florida by Wood (1988), 37.6% are in Fakahatchee Strand State Preserve. Everglades National Park has fewer, with some 27% of the total. Southern Florida perhaps has more endangered species than any area east of Texas; perhaps even more than that state (D. B. Ward, pers. comm.).

## ACKNOWLEDGMENTS

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# NEW ENGLAND NOTE

## *CAREX AESTIVALIS* IN VERMONT

PETER F. ZIKA AND JERRY C. JENKINS

*Carex aestivalis* M. A. Curtis, the summer sedge, was discovered in Vermont in 1903, in dry limy woods along Broad Brook in South Pownal, Bennington Co. (Churchill, 1905). In 1904 a second Vermont station was located on Mt. Herrick, Ira, Rutland Co. (*Carpenter s.n.*, VT). Despite the prolific sedge collecting of Flynn, Pringle, Brainerd, Ross, Knowlton, Atwood, Seymour and others, no additional stations for *C. aestivalis* were recorded after 1904 in Vermont.

In 1981 we encountered a population of about 1000 *Carex aestivalis* in limy, rocky woods on the east slope of Mt. Equinox, Manchester, Bennington Co. (*Zika and Jenkins 3867, 3891,* BEDF, NEBC, VT). The site is in Cook Hollow, at an elevation of 2300 feet. Most of the plants seen were fruiting in the first week of July. Summer sedge was shaded by *Acer saccharum* Marsh., and growing with *Agropyron trachycaulon* (Link) Malte ex H. F. Lewis, *Arabis canadensis* L., *Carex rosea* Schkuhr, *C. sparganioides* Muhl., *Festuca obtusa* Biehler, and a diverse community of other herbaceous plants. The bedrock was Ordovician limestone in the Bascom formation (Doll et al., 1961).

In 1989 a second population of summer sedge was located along the Long Trail, about one-quarter mile north of the Route 9 crossing in Woodford, Bennington Co. (*Zika 10668,* VT). About 30 widely scattered plants were seen, primarily in a sunny area of recent blowdowns, but also in the forest upslope. The bedrock was Precambrian gneiss in the Mt. Holly complex (Doll et al., 1961). The population was centered at an elevation of roughly 1500 feet on the south-facing slope of Maple Hill. The canopy was *Acer saccharum, Betula alleghanensis* Britt., *Fagus grandifolia* Ehrh., and *Fraxinus americana* L.; associated species included *Carex brunnescens* (Pers.) Poir., *C. communis* Bailey, *C. deweyana* Schwein., *C. debilis* Michx., *C. intumescens* Rudge, and *Viola canadensis* L.

The writers have unsucessfully attempted several times to locate Churchill's station; whether Carpenter's colony is still extant is not known.

While summer sedge is certainly rare in Vermont, we do not believe the species is threatened or endangered, and do not recommend it for legal protection under state law (10 V. S. A., Chapter 123) at this time. We believe "special concern" status is more appropriate. "Special concern" is a category without legal status, created by the Vermont Endangered Species Committee for species requiring more study before listing as theatened or endangered. *Carex aestivalis* is an inconspicuous species that may have been overlooked in southwestern Vermont in limy woods. It is superficially similar to *C. gracillima* Schwein. and *C. arctata* Boott ex Hook., common woodland species. More field work is needed to determine the status of summer sedge in Vermont. South of Vermont *C. aestivalis* is widespread.

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RHODORA, Vol. 92, No. 869, pp. 38–41, 1990

## NEW ENGLAND NOTE

# REDISCOVERY OF SOME RARE PLANTS ON MT. KATAHDIN

ALISON C. DIBBLE, SALLY C. ROONEY, HAROLD HINDS, W. DONALD HUDSON, JR., AND BRUCE A. SORRIE

In 1988, the Maine Herbarium of the University of Maine, Orono (ME) organized several botanical explorations of Mt. Katahdin in Baxter State Park, Piscataquis County, Maine for the purpose of re-locating plants not seen for at least twenty years. This effort was prompted by the recent establishment of Maine's Official List of Endangered and Threatened Plants (Dibble et al., 1989). The expeditions involved three trips: a small party went on a preliminary trip on May 27–29; a larger group went on June 24–26; and A. Dibble returned on July 29–31.[1] Taxonomy in this report follows Fernald (1970), Kartesz and Kartesz (1980) and Hudson (1987).

The areas investigated by these parties include North Basin Pond, South Basin Pond, Depot Pond, Dry Pond, Chimney Pond, Saddle Trail, the head of Saddle Slide, the Cutoff Trail between Great Basin and North Basin, the Tableland from North Basin to the head of Abol Slide, and North Basin.

The most noteworthy plants rediscovered as a result of these efforts are *Carex katahdinensis* Fern., *Carex* ×*mainensis* Porter, and *Euphrasia oakesii* Wettst. *Carex katahdinensis*, not seen on Mt. Katahdin since 1900 when M. L. Fernald described it from a site at the gravelly margin of a small pond (Fernald, 1901; Williams, 1901; Hudson, 1988), was spotted by H. Hinds. *Carex* ×*mainensis*, reputedly a sterile hybrid between *C. saxatilis* var. *miliaris* or *C. s.* var. *rhomalea* and *C. vesicaria* (Fernald, 1901, 1970; Scoggan, 1978), or between *C. rostrata* and *C. saxatilis* var. ?*rhomalea* (Scoggan, 1978), had also not been seen since 1900 (Critical Areas Program, 1985). Dibble rediscovered *C.* ×*mainensis* in late July when she revisited the pond to check on the

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[1] Participants in the expedition were Christopher S. Campbell, Patricia E. DeHond, Scott Drummond, Betsy Knight, Patricia Ledlie, Candace McKellar, Janet S. McMahon, Constance S. Stubbs, Jill E. Weber, Andrew A. Whitman, Garret Van Wart, and the authors.

mature *C. katahdinensis,* with which it occurs. *Euphrasia oakesii,* a diminutive plant less than 2 cm tall, had not been seen since Fernald's record of July 11, 1900. Hudson, who had been searching for this plant for twelve years, spotted it at the base of a seepy escarpment in the remote North Basin. Apparently this plant is extremely local, occurring in an area about 1 m square. It is probable that sites for all three of the above species are the historic locations from which Fernald (1901) made his collections.

In the North Basin, Sorrie found a new subpopulation of *Saxifraga stellaris* L. var. *comosa* Retz. (= *S. foliolosa* R. Br. var. *foliolosa*), which is found in the eastern United States only on Mt. Katahdin. Hudson's (1987) work on the reproductive biology of this taxon has involved observation of three other small subpopulations there.

Two species, *Carex katahdinensis* and *Euphrasia oakesii* had been listed as Possibly Extirpated in Maine's Official List of Endangered and Threatened Plants (Dibble et al., 1989) but because of their re-location are now given state Endangered status.

Other plants of interest seen in 1988 included 15 State Endangered taxa (having a single known population in Maine), known in the state only from Mt. Katahdin. These taxa are *Lycopodium sitchense* Rupr., *Poa fernaldiana* Nannf., *Carex saxatilis* L., *Luzula spicata* (L.) DC., *Salix herbacea* L., *Salix planifolia* Pursh, *Betula glandulosa* Michx., *Betula minor* (Tuckerman) Fern., *Viola palustris* L., *Cassiope hypnoides* (L.) D. Don, *Loiseleuria procumbens* (L.) Desv., *Phyllodoce caerulea* (L.) Bab., *Rhodendron lapponicum* (L.) Wahlenb., *Spiraea septentrionalis* (Fern.) Love & Love (= *S. latifolia* var. *s.*) and *Prenanthes nana* (Bigelow) Torr. Six State Threatened plants (having 2–4 documented, recent occurrences in Maine) were seen: *Hierochloe alpina* (Willd.) Roemer & Schultes, *Carex scirpoidea* Michx., *Salix uva-ursi* Pursh, *Arctostaphylos alpina* (L.) Spreng., *Epilobium hornemannii* Reichenb. and *Prenanthes boottii* (DC.) Gray. Six plants of Special Concern status (having 5–10 occurrences) were seen: *Lycopodium selago* L., *Agrostis mertensii* Trin. (= *A. borealis* Hartman), *Carex atratiformis* Britt., *Carex bigelowii* Torr., *Geocaulon lividum* (Richards) Fern. and *Arnica mollis* Hook. Four Watch List species (having more than 10 occurrences, but of concern) were seen: *Juncus trifidus* L., *Castilleja septentrionalis* Lindl., *Minuartia groenlandica* (Retz.) Ostenf. and *Viburnum edule* (Michx.) Raf. In addition, some plants not often found in Maine and not cur-

rently on Maine's Official List were seen in 1988. These include *Orobanche uniflora* L., *Senecio pauperculus* Michx. and *Viola labradorica* Schrank.

Known to have occurred on Mt. Katahdin (Churchill, 1901; Fernald, 1901; Harvey, 1903; Hudson, 1988) but not seen in 1988 are the following: *Potamogeton confervoides* Reichenb., *Deschampsia atropurpurea* (Wahlenb.) Scheele, *Festuca rubra* L. var. *Prolifera* Piper, *Phleum alpinum* L., *Trisetum triflorum* (Bigelow) Love & Love (= *T. spicatum* var. *pilosiglume*), *Carex rariflora* (Wahlenb.) Sm., *Luzula confusa* Lindeberg, *Listera auriculata* Wieg., *Salix arctophila* Cockerell *ex* Heller, *Salix argyrocarpa* Anderss., *Polygonum viviparum* L., *Silene acaulis* (L.) Jacq. var. *acaulis* (= *S. a.* var. *exscapa*), *Cardamine bellidifolia* L., *Draba allenii* Fern. (= *D. lactea* M. F. Adams), *Saxifraga paniculata* P. Mill. (= *S. aizoon* var. *neogaea*), *Epilobium anagallidifolium* Lam. (= *E. alpinum*), *Veronica wormskjoldii* Roemer & Schultes (= *V. alpina* var. *unalaschensis*) and *Gnaphalium supinum* L.

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RHODORA, Vol. 92, No. 869, pp. 42–44, 1990

HISTORICAL NOTE

# NOTES ON THE DIFFICULTIES EXPERIENCED BY SPRUCE IN HIS COLLECTING

RICHARD EVANS SCHULTES

Although the work of the outstanding British plant collector of the Amazon and Andes, Richard Spruce, is well documented in Wallace's 2-volume *Notes of a Botanist on the Amazon and Andes* (Spruce, 1908), edited primarily on the basis of letters and notes of the great plant explorer after his death, there is still unpublished material in the Royal Botanic Gardens, Kew, and the Linnean Society of London. This material leaves little doubt that Spruce was a tireless worker, that he probably preferred to work alone and that, although his dedication to floristic and taxonomic research left him little free time, he was interested in ethnobotany and in the knowledge that Indians had of their flora and in their ways of life.

From a letter to Mr. Bentham sent from Manáos, dated April 1, 1851, it is possible to see one of these characteristics of the man and his methods of work:

> "My dear Sir–
>
> I write to request you to pay to Mr. King (who is leaving me) the sum of £30 and to place the same to my account. I have given him an order upon which you will probably receive nearly at the same time as this.—Men are not very easy to obtain here, but I can do nearly as much alone as we two have mostly done, until I meet with some one to suit me. The person who is now leaving me has been a continual drag on my movements, and for some time past, when any excursion has been likely to entail difficulty or danger, I have gone alone rather than be troubled by him."

Spruce's difficulties resulting from Indian celebrations, dances and festivals, and cataracts to pass without adequate help were frequent and serious and often entered into his field notes and letters. I can sympathize with Spruce: both of us, dedicated to use

every precious moment in botanical research and collection, found it difficult to adjust to this so different aspect of Indian life-style.

The falls of São Gabriel at the junction of the Río Negro and Río Vaupés were the subject of these two notes, the first dated December 28, 1851, the second April 15, 1852.

"Thus, far, have I advanced into the bowels of the land without impediment, and before adventuring the falls (where I may possibly get a ducking) I seize an opportunity of sending you the seeds of a beautiful Lythraceous tree which I collected on the way up. . . . "The Río Negro might be called the Dead River.—I never saw such a deserted region—in S. Isabel & Castanheira there was not a soul as I came up, and three towns marked on the most modern map I have, have altogether disappeared from the face of the earth."

São Gabriel, Río Negro. April 15, 1852.

". . . It is not pleasant to work here to be always among cataracts in my excursions. . . . I was out 4 days but 2 of them were lost time. I made my station at the house of the pilot of the falls, at the foot of the latter, and arrived just in time before the commencement of one of their great 'festas.' Much against my will I was compelled also to see the end of it, for no one wd stir until after two days of drinking and 2 nights of dancing. I was interested to hear the legend of the discovery of the mandiocca-root sung in the Barré language, and this was poor consolation for such a loss of time, and you may imagine how I fretted in my imprisonment on a small rocky island begirt with foaming waters, where I could not find a single flower that I had not already gathered."

As if his problems on the rivers of the northwest Amazon were not enough, he encountered further difficulties in his botanically rich trip up the eastern slopes of Ecuador and Peru to arrive finally in Quito. In a letter written from Baños, at the headwaters of the Río Pastaza (presumably to Mr. Hooker) and dated July 4, 1857, Spruce wrote the following brief account of his problems:

"Dear Sir–I have at length the pleasure of writing to you from the Quitenian Andes—the goal so long placed before my eyes at an apparently interminable distance. I reached Baños 2 days ago after a most wearisome and perilous journey of 3 months, the worst part of which has been the last 18 days, occupied in traversing the Montaña from Canelos, at the head of the Bombanasa—the same forest that gave such trouble to Gonzalo Pizarro and Orellano 300 years ago—as wild as it was then, and containing fewer inhabitants, for there are but 6 huts of unconverted Indians (Jivaros) about midway of it."

## ACKNOWLEDGMENTS

I wish to acknowledge the courtesy of the Director of the Royal Botanic Gardens, Kew, and the offices of the Linnean Society of London for permission to publish these notes from their archives.

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## XVTH INTERNATIONAL BOTANICAL CONGRESS 1993

The Organizing Committee of the XVth International Botanical Congress wishes to announce that the XV IBC will be held in the Tokyo area during August and September, 1993: nomenclature session 23–27 August; general session 28 August–3 September. The first circular of the XV IBC will be prepared in 1990 and distributed to those are are interested in the Congress. Request for information and other questions and comments may be sent to the Secretariat at the following address:

XV International Botanical Congress Tokyo
Department of Botany, Faculty of Science
The University of Tokyo, 7-3-1 Hongo
Bunkyo-ku, Tokyo 113, JAPAN

---

## MEETING ANNOUNCEMENT AND CALL FOR ABSTRACTS NEW ENGLAND BOTANY GRADUATE STUDENTS

The fifth New England Botany Graduate Student Meeting will be hosted by the Department of Botany and Plant Pathology at the University of Maine, Orono, ME on Saturday, 14 April 1990. Attendance is open to all. Paper presentations will be largely restricted to graduate student research (completed or in progress) representing all areas of botany (systematics, ecology, reproductive biology, anatomy, physiology, etc.). Time slots for paper presentations are limited and prior registration is required. Abstracts are due by Wednesday, 14 March 1990.

For information and abstract forms, contact Alison C. Dibble, Thomas Mione or Jeannette Whitton, organizers.

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THE NEW ENGLAND BOTANICAL CLUB
22 Divinity Avenue
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The New England Botanical Club is a non-profit organization that promotes the study of plants of North America, especially the flora of New England and adjacent areas. The Club holds regular meetings, has a large herbarium of New England plants, and a library. It publishes a quarterly journal, RHODORA, which is now in its 91st year and contains about 500 pages a volume.

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RHODORA January 1990 Vol. 92, No. 869

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# Rhodora

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Vol. 92 April 1990 No. 870

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# RHODORA



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**Cover Illustration**

*Sabatia kennedyana* Fern. (Plymouth Gentian). A globally rare, disjunct species of the coastal plain of North America, occurring in northeastern South Carolina, southeastern North Carolina, southeastern New England, and Yarmouth County, Nova Scotia. Original artwork by Tess Feltes; from *New England's Rare, Threatened and Endangered Plants*. Crow, G. E. 1982. Reproduced by permission.

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RHODORA, Vol. 92, No. 870, pp. 47–49, 1990

# A NEW FORM OF *CYPRIPEDIUM MONTANUM* DOUGL. EX LINDL.[1]

CHARLES J. SHEVIAK

ABSTRACT

A rare color-form of *Cypripedium montanum* Dougl. ex Lindl., characterized by clear green sepals and petals and unmarked lip and staminode, is described as forma *praetertinctum* Sheviak.

Key Words: *Cypripedium montanum*, color-form, western North America

*Cypripedium montanum* Dougl. ex Lindl f. *montanum* is characterized by a white lip marked internally with magenta, dark reddish-brown sepals and petals, and a yellow staminode with reddish spots. Herbarium work conducted in conjunction with a study of the *C. calceolus* L. complex disclosed a single specimen evidently referable to *C. montanum*, but differing from typical plants of this species in its clear green sepals and petals totally lacking dark pigmentation. These characteristics suggest that this specimen represents a rare but predictable color-form of *C. montanum*. Field work in Alberta and British Columbia during June and July of 1989 disclosed another such plant and confirmed this hypothesis.

In one of several large colonies of *Cypripedium montanum* studied over an area extending for some tens of kilometers, a single plant was found lacking any evidence of reddish pigmentation in the flower. The sepals and petals were clear, light green, without the suffusion of dark reddish brown characteristic of the species and present in all other individuals seen throughout the

[1] Contribution number 639 of the New York State Science Service.



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region. The lip was pure white, lacking internal magenta markings and the staminode was clear yellow without reddish spots.

This new form is here formally described in part to facilitate the discussion of interspecific variation in the group.

**Cypripedium montanum** Dougl. ex Lindl. forma **praetertinctum** Sheviak

A forma montana floribus sine rubellipigmento (sepalis et petalis viridibus, labello et staminodio immaculato) differt.

Differing from forma *montanum* in its flowers lacking all reddish pigmentation: sepals and petals clear green, lip pure white without magenta markings, and staminode yellow without reddish spots.

TYPE. CANADA: British Columbia: Dry, open, mostly barren eroding bank in spruce-fir forest. Radium. 29 June 1989. *C. J. Sheviak, J. K. Sheviak, & W. F. Metzlaff 3109/2* (HOLOTYPE: NYS).

ADDITIONAL SPECIMEN. U.S.A.: Oregon: Lane Co.: McKenzie Hwy. May 1932. *S. Warg s.n.* (OSC 32914).

ETYMOLOGY. From *praeter* (passed by, without [signifying exclusion]) and *tinctum,* past participle of *tingere* (to dye or stain).

In flowers of *Cypripedium montanum* f. *montanum,* perceived differences in the reddish colors of sepals, petals, lip, and staminode apparently arise from the differences in pigments of other colors present in the various organs, and perhaps physical factors, rather than from differences in the reddish pigments themselves. Under magnification, the reddish coloring of the sepals and petals and the spots on the staminode can be seen to be similar in hue to the magenta markings of the lip, and, indeed, the total lack of these colors in f. *praetertinctum* indicates a relationship between the reddish pigments in the different floral organs. Such a pattern of pigmentation is well-known in the genus, and some other species with typically reddish-pigmented flowers exhibit forms with flowers bearing white lips and green sepals and petals (e.g., *C. acaule* Ait. f. *albiflorum* Rand & Redfield; *C. arietinum* R.Br. f. *albiflorum* House).

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I am indebted to W. F. Metzlaff, Calgary, and G. Preusse, Red Deer, Alberta, for their generous assistance in the field and for their warm hospitality. I wish to thank the curators and staffs of the herbaria that lent western specimens or provided facilities during my visits: ALA, COLO, CS, ID, JEPS, OSC/WILLU, RM, UBC, UC, WS, and WTU.

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# SCENTED ANTHERS IN THE SOLANACEAE

WILLIAM G. D'ARCY, NANCY S. D'ARCY,
AND RICHARD C. KEATING

## ABSTRACT

Anthers and corollas from fresh flowers of 27 taxa of Solanaceae were separately stored in jars and then smelled. The anthers nearly always produced scents, but the corollas often did not, and when present, the corolla scents were different from those of the anthers. We hypothesize that the anther scents are related to bee pollination and are a basal, conservative feature of the Solanaceae, while the corolla scents represent specializations to attract other pollinators.

Key Words: anthers, floral scents, pollination, Solanaceae, world-wide representatives

We have found that Solanaceous anthers emit scents that are different from those sometimes found in the corollas. The anther scents seem to be localized on pollen. The taxonomic distribution of the scents produced suggests that the anther scents may be conservative within the family.

Our sample (Table 1) of Solanaceae was of 27 taxa in 16 genera. including representatives from both major subfamilies and from several tribes. Anthers and corollas from several (usually 5–10) freshly opened flowers of different taxa were placed separately in new Baxter Snap-Cap specimen bottles[1] and stored for 2–8 hours to concentrate floral odors so they that could be detected by the human nose. In all attempts, odors were detected in the samples with longitudinally dehiscent anthers, and they were almost always different from scents found in corollas. When anthers of species with poricidal dehiscence were coarsely chopped with a razor blade to expose the interiors before storing in the specimen jars, they too emited odors. There was only one exception: the pistillate flower of *Solanum polygamum,* which lacks pollen, yielded no detectable odor. The smelling of the jars was done by the authors and several others over a two-week period.

Some of the scents detected were of a "standard" nature and others were sweet. What we refer to as the "standard anther odor," found only in anthers, is difficult to characterize, but was thought

[1] Baxter Healthcare Corporation, Scientific Products Division, 1430 Waukegan Road, McGaw Park, IL 60085–6787.

Table 1. Anthers tried for smell test.

| Taxon | Anther | Corolla | Notes |
|---|---|---|---|
| *Acnistus arborescens* | standard | none | |
| *Brugmansia 'rosea'* | standard | floral | weak |
| *Brunfelsia mire* | standard | floral | |
| *Brunfelsia pauciflora* | standard | floral | |
| *Brunfelsia undulata* | floral | floral | strong |
| *Capsicum annuum* | standard | none | slightly sweet |
| *Cestrum nocturnum* | standard | floral | weak |
| *Datura stramonium* | standard | floral | weak |
| *Iochroma cyaneum* | standard | none | |
| *Iochroma fuchsioides* | standard | none | |
| *Leucophysalis grandiflora* | weak | none | distinctive |
| #*Lycianthes* aff. *heteroclita* | weak | none | |
| *Nierembergia hippomanica* | standard | none | |
| *Petunia hybrida*-1 | standard | none | |
| *Petunia hybrida*-2 | standard | perfume | |
| *Physalis alkekengi* | standard | none | |
| *Salpichroa origanifolia* | standard | none | |
| *Solanum americanum* | none | none | |
| #*Solanum americanum* | standard | none | weak |
| #*Solanum laciniatum* | perfume | none | |
| #*Solanum mahoriensis* | perfume | none | |
| #*Solanum polygamum* | none | none | |
| #*Solanum pyracanthos* | standard | none | slightly spicy |
| #*Solanum racemosum* | standard | none | |
| #*Solanum rudepannum* | fruity | none | |
| *Vassobia breviflora* | standard | none | sweet |
| *Witheringia correae* | standard | — | |
| *Witheringia solancea* | standard | none | weak |

# Anthers coarsely chopped.
— Not assessed.
27 taxa of Solanaceae in 16 genera.

to be distinctive and not to resemble any floral or fruit fragrances or the "green" odors often associated with crushed foliage. The standard anther odor differed slightly in different taxa, but was always identifiable and similar. In many taxa, corollas yielded no odors, but those that did tended to have sweet scents resembling those of perfumery. Odors were not detected before the anthers opened, and they diminished in samples taken one or two days after flower opening.

Our sample, although limited, does include a taxonomic range that suggests that anther scents are general if not universal in the

family. Our sampling showed that many species have two scent systems, one in the anther and another in the corolla, each producing quite different scents.

This work substantiates earlier reports of scents in the anthers of angiosperms (Percival, 1965) and scented pollen in the Solanaceae (Buchmann, 1983). Our methodology in recording these scents is subjective but easily repeatable. Such subjectivity is commonly accepted in observations of colors, insect sounds, and textures of many objects. We hope that more precise methodology will later permit better description to facilitate further use and expanded inferences from these results and suggest the site and mechanisms of fragrance production. We think that the fragrances are related to pollination, as scents are well known to be pollinator attractants in flowering plants, and we assume that the small amounts of scent emitted by these anthers can be effective in attracting pollinators.

Fragrance, often night-timed, is well known in many Solanaceae, for example, *Cestrum nocturnum,* varieties of *Petunia hybrida,* cultivated species of *Nicotiana,* and some species of *Brunfelsia.* These strong fragrances are produced on the corolla (Table 1). In *Brunfelsia,* only the more advanced sections of the genus, which is normally butterfly or hawkmoth pollinated, have such corolla scents (Plowman, 1973, Ph.D. thesis, Harvard University). In contrast, some species of *Iochroma* (Table 1), which have tubular red or blue flowers and are presumably hummingbird-pollinated, lack corolla scents. It is interesting that all of these, *Cestrum,* the petunias, the nicotianas, the brunfelsias, and the iochromas, have anthers with what we term the standard scent. Only *Brunfelsia undulata* had a similar odor in both anthers and corolla.

Although the Solanaceae are pollinated in a variety of ways, poricidal species adapted to buzz pollination (Buchmann, 1983) comprise more than half the species in the family (D'Arcy, 1990), and many of the genera with longitudinal dehiscence are also visited by bees. Because the standard anther odor is present in a wide range of taxa, we suggest that it is related to bee pollination and we also suggest that it may be basal in the evolution of the family.

*Solanum* sect. *Leptostemonum* has a number of adaptations that may be looked upon as specializations, e.g., cauline and foliar spines, stellate hairs, and attenuate anthers with small pores. Some

members of this subgenus depart from the standard anther odor condition in having sweetly fragrant anthers, which may also be a specialization. It would be interesting to us to know whether the pollinators of *Solanum* sect. *Leptostemonum,* differ from the bee pollinators that visit flowers with the standard anther scent.

If the Solanaceae are primarily or ancestrally bee-pollinated, the development of scent, color, and shape innovations to attract new pollinators has generally not been accompanied by a reduction or disappearance of the anther scent system which may be basal in the family and involved in attraction of basic bee pollinators. Hence the standard anther scent system distributed across much of the family might be thought of as a conservative pollination attribute of members of the Solanaceae.

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# OBSERVATIONS ON THE FLORAL SHOOTS OF *MONOTROPA HYPOPITYS* (MONOTROPACEAE)

A. Randall Olson

*Monotropa* is one of ten achlorophyllous, obligate mycotrophic genera in the Monotropaceae (Cronquist, 1981). Members of this genus basically exist as perennial root masses associated with and completely dependent upon their mycorrhizal fungi in mixed and coniferous forests. The only aerial portions of this taxon are bracteate, nodding floral shoots which arise directly from the root system and become erect during fruit development. One of the major characters used to separate the two species is the flower number associated with each above-ground axis. *Monotropa uniflora* L., as the name indicates, consistently produces a single, terminal flower; *M. hypopitys* L. usually produces a raceme-like inflorescence bearing several flowers, but a number of single flowered specimens have been reported (Wallace, 1975). Aerial shoots of *M. hypopitys* bearing a single flower suggest that this character may be of limited taxonomic use in certain circumstances.

A small population of *Monotropa hypopitys* located in a moist, coniferous forest in central Colchester County, Nova Scotia, Canada has been monitored over the past five years. The number of aerial shoots produced from year to year is extremely variable. In July 1988, two single-flowered shoots were observed to be relatively smaller and thinner than the multiflowered shoots in the vicinity. One of the single-flowered shoots eventually succumbed to a fungal disease; the other single-flowered specimen was collected and fixed in FAA (formalin-acetic-acid-alcohol) for preservation in the wet collection of the A.E. Roland Herbarium. For the purposes of this note, a floriferous bract is defined as having either a functional flower in its axil or an aborted flower bud in its axil. Sterile bracts have neither structure associated with their axils.

Dissection and study of the preserved single-flowered specimen of *Monotropa hypopitys* revealed the presence of a lateral, aborted flower bud in the axil of each of three bracts inserted below the functional, terminal flower at the distal end of the shoot. Figure 1 illustrates a portion of the terminal flower, a sterile bract, and the first of the three floriferous bracts with an aborted bud. Subsequent examinations of herbarium and fresh material indicate

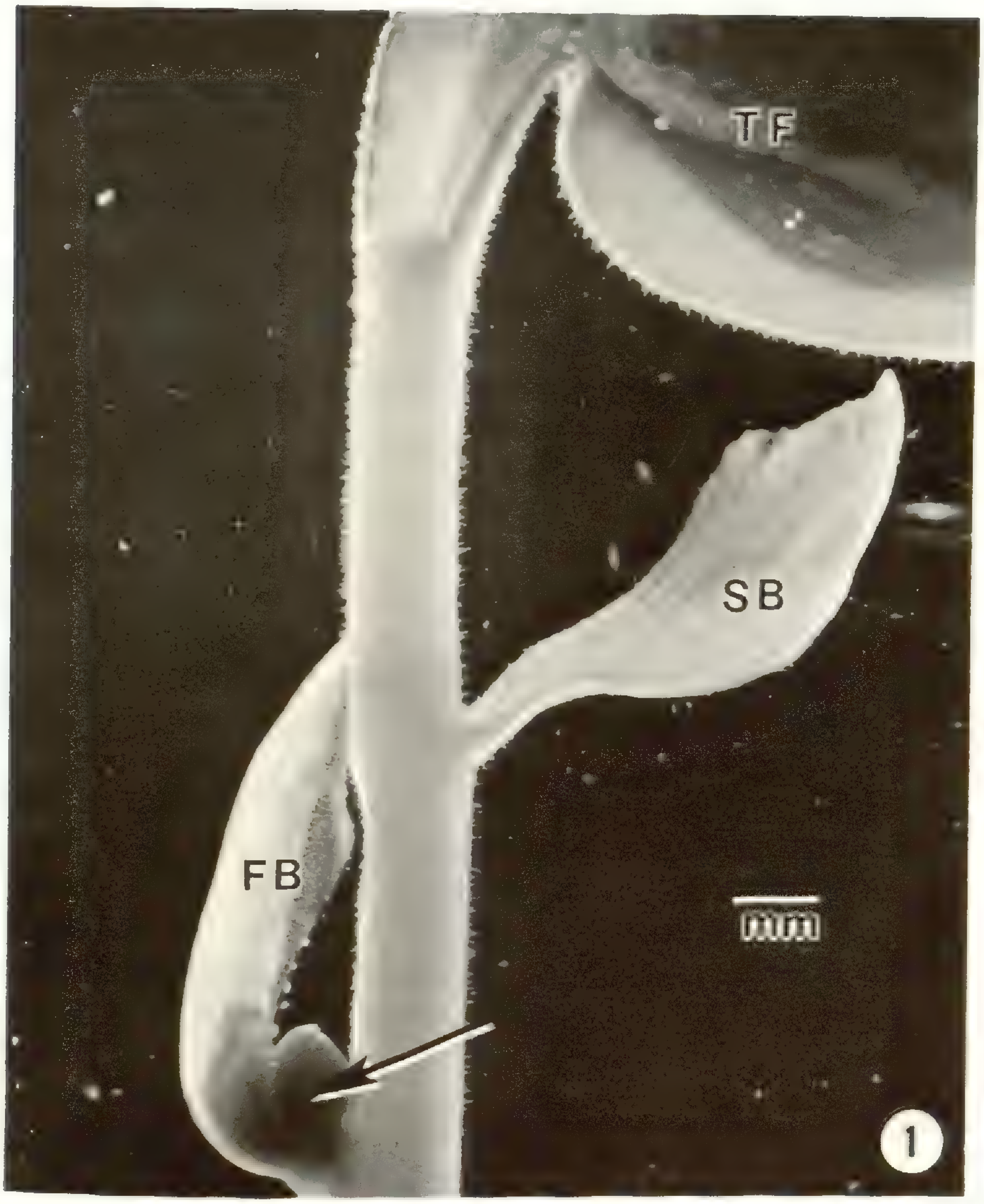


Figure 1. *Monotropa hypopitys* L. Arrow indicates an aborted flower bud in the axil of a lateral bract. FB = floriferous bract; SB = sterile bract; TF = terminal flower.

that a significant number of multiflowered aerial shoots in a population also produce a variable number of bracts with an aborted flower bud in the axil (Olson, unpubl.). Out of a total of 16 aerial shoots produced by the same population in July 1989, all but one shoot had formed at least one aborted bud in the axil of a lateral bract in addition to those lateral bracts with a functional open flower.

To date, there are no reports of *Monotropa uniflora* producing

more than a single, terminal flower, whereas *M. hypopitys* appears consistently to produce multiple floriferous bracts with either a functional flower or an aborted bud in the axil. If these observations are verified from careful developmental and field studies, the number of potential flowers as indicated by the presence of only one or more than one floriferous bract may be a reliable and, therefore, useful distinguishing character between these two taxa.

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# GEOGRAPHIC VARIATION IN ALKALOID CONTENT OF *SANGUINARIA CANADENSIS* (PAPAVERACEAE)

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## ABSTRACT

We sampled *Sanguinaria canadensis* L. (bloodroot) rhizomes from 100 eastern U.S. populations to assess variation in the alkaloid sanguinarine. Sanguinarine content varied from 0.6% to 6.3% of rhizome dry weight (mean 2.7%). This variation correlates with latitude, longitude, slope, clay content, litter depth, rhizome size, and fruit size. A regression with latitude, pH, and percent humic matter accounted for 58% of the alkaloid variation among populations. Alkaloid concentrations also vary seasonally. Highest alkaloid levels occurred during flowering and fruiting stages.

Key Words: *Sanguinaria canadensis,* alkaloids, sanguinarine, bloodroot, geographic variation, rhizome, eastern U.S.

Alkaloids occur in more than 300 plant families (Li and Willaman, 1972) and are particularly abundant in Fabaceae, Papaveraceae, Ranunculaceae, and Solanaceae. The function of these secondary metabolites is uncertain. They may be metabolic wastes, nitrogen storage compounds, plant pigments, biochemical regulators, plant growth substances, or defense compounds (Robinson, 1974, 1979; Seigler, 1977; Waller and Nowacki, 1978; Rhoades, 1979). Despite their uncertain biological role, alkaloid synthesis requires substantial metabolic investments. Nicotine production in tobacco may require 10% of the plant's metabolic output (Robinson, 1974).

*Sanguinaria canadensis* L., a monotypic, alkaloid-bearing member of Papaveraceae, grows throughout the eastern and midwestern U.S. (Ernst, 1962). One of the earliest spring-flowering species, *Sanguinaria* is most abundant on cool, moist, well-drained, wooded slopes. Rhizomes produce one or two leaves, each borne on an elongate petiole. Both the generic name, *Sanguinaria,* and the common name, bloodroot, describe the deep orange-red latex found in the rhizome. The color is due to the water-soluble, benzophenanthridine alkaloid sanguinarine.

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Sanguinarine inhibits growth of *Phymatotrichum omnivorum* (Shear) Duggar, the fungus responsible for root rot, at concentrations as low as 2.5 ppm (Greathouse, 1939). Greathouse and Rigler (1940) found it the most effective of 62 alkaloids tested against *P. omnivorum*. Sanguinarine also may be effective against bacteria, human pathogenic fungi, parasitic protozoans, viruses, and cancerous tissue (*see* Howell et al., 1973).

Traditional bloodroot uses include stimulants, expectorants, and emetics (Martin et al., 1961; Lewis and Lewis, 1977). There is renewed interest in sanguinarine because of its bactericidal and bacteriostatic properties against oral plaque-forming organisms (Dzink and Socransky, 1985) Sanguinarine is the active, anti-plaque agent in an oral rinse and tooth paste produced by Vipont Laboratories.

Infraspecific variation of secondary metabolites is common and may correlate with geographic clines or environmental conditions. Levin and York (1978) discussed examples of clinical variation in alkaloid content and stated, "presumably these clines are the result of natural selection." Levin (1976) noted two distinct trends: more annual than perennial alkaloid-bearing plants, and a negative correlation between the incidence of alkaloids and latitude. Seasonal, diurnal and intrapopulational differences are also known (*see* Harborne and Turner, 1984). Here we describe variability of sanguinarine content in 100 populations of *S. canadensis* and discuss environmental and morphological correlations.

## MATERIALS AND METHODS

We sampled one hundred *Sanguinaria canadensis* populations from North Carolina to southern Vermont, and west to Indiana. We collected plants from mid-spring to late summer of 1983, beginning in the southern Appalachians and working north. Though collection dates varied, we sampled all populations at equivalent phenological stages (late fruit). Subsequently, we re-sampled several populations during post-fruiting (mid-summer) and late season stages just before leaf senescence (early fall) and then in early flowering stages the following spring (1984).

We collected 10–40 bloodroot plants from each population and recorded rhizome, leaf, capsule dimensions, pedicel length, and rhizome weights for five specimens bearing fully-expanded leaves. To make a sample large enough for chemical analysis, we com-

bined the five measured rhizomes. We also analyzed the second sample from each population (5–35 rhizomes) but did not record leaf measurements for these.

The North Carolina Department of Agriculture in Raleigh analyzed a composite soil sample from each population. In the field we estimated soil structure and clay content and determined pH colorimetrically. We also determined slope, aspect, elevation, depth of litter, parent rock, and species composition of the canopy for each site.

We dried rhizomes beneath low-temperature lights, then determined alkaloid concentrations at Vipont Laboratories in Ft. Collins, CO following analytical methods described by Boulware et al. (1984). Previous studies have shown that once dried, bloodroot's alkaloid constituents are stable (Boulware, unpubl. data). We performed analysis of variance and regressions using SAS (Goodnight et al., 1982) at the University of North Carolina at Chapel Hill.

## RESULTS

Several alkaloids are identifiable in bloodroot rhizomes but sanguinarine is dominant, making up at least 50% of the total. Sanguinarine concentrations of sampled rhizomes ranged from .6% to 6.3% of rhizome dry weight. We recently found a population with 9% sanguinarine content but did not include it with this analysis. The average sanguinarine concentration was 2.7%, similar to that from commercial (foraged or wild collected) rhizomes sold in the pharmaceutical crude-drug markets. Collection sites are shown in the map (Figure 1).

We found significant correlations between sanguinarine levels and five of six continuous environmental and geographic variables (Table 1A). The strongest correlation was with longitude ($r = .60$). Latitude was negatively correlated with sanguinarine content ($r = -.40$). North of the Pennsylvania-West Virginia border there was a rather abrupt decline. *Sanguinaria* populations from Pennsylvania, New York and Vermont had very low concentrations (Figure 1). We detected no relationship between population size and vigor except that two of the highest alkaloid concentrations occurred in small, isolated populations. Clay content, slope, and litter depth also were correlated positively with sanguinarine concentrations ($r = .34$–$.36$).

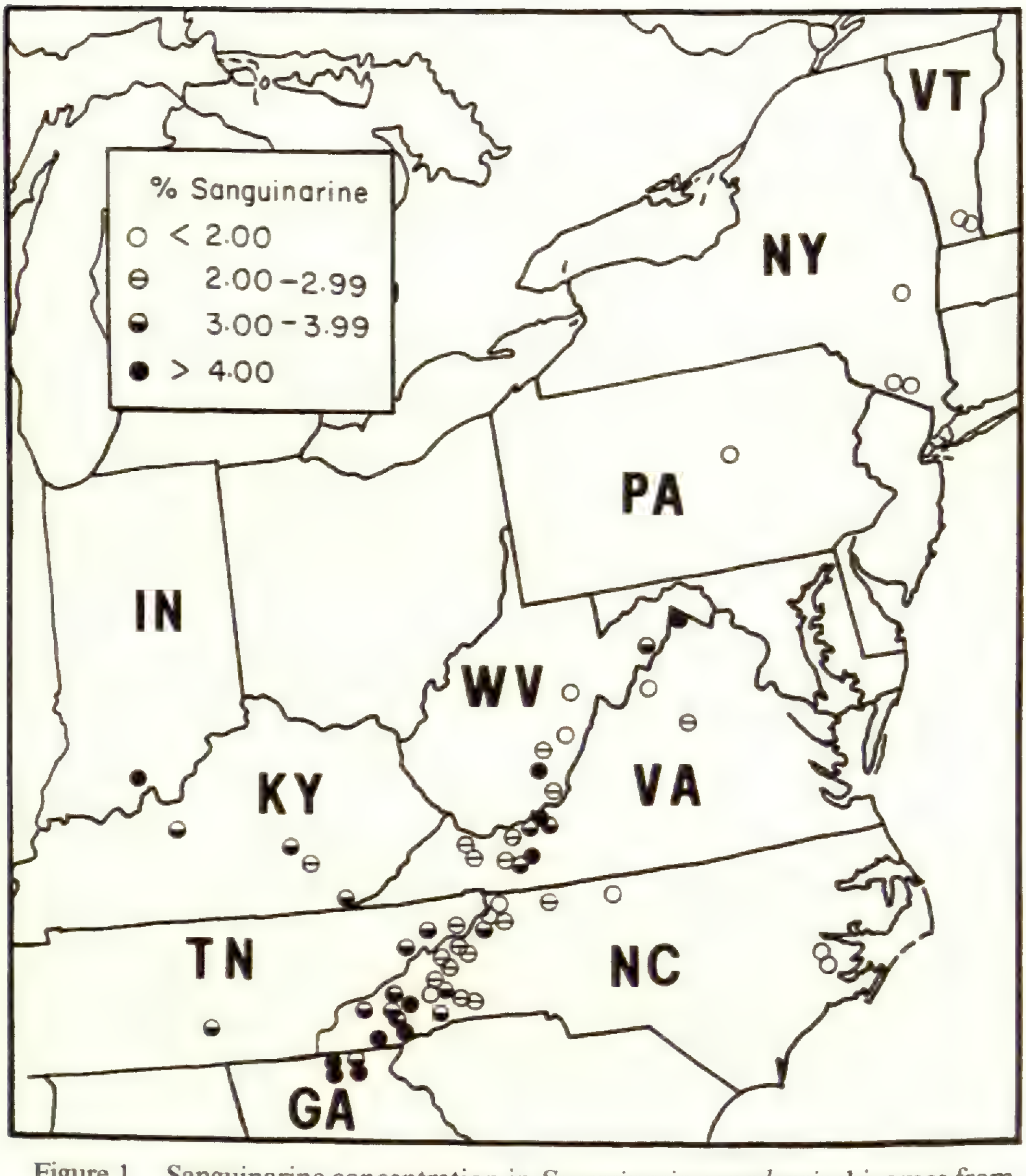



Figure 1. Sanguinarine concentration in *Sanguinaria canadensis* rhizomes from eastern U.S. sites.

Sanguinarine was correlated negatively with P and Cu but not with nine additional soil variables measured (Table 1B). We classified soils as structured (crumbly, blocky, or platy) or unstructured (massive) and included loamy soils with structured clays. Rhizomes from structured soils had a significantly greater mean sanguinarine content (Table 2).

No significant correlations occurred between leaf variables (length, width and petiole length) and sanguinarine content. However, fresh rhizome weight and volume (calculated from length

Table 1. Pearson Product Moment Correlation analysis. Rhizome sanguinarine content (% of dry weight) with all continuous variables. ($n$ = number of observations, $r$ = correlation coefficient, $P$ = probability; CEC = cation exchange capacity, BSP = percent base saturation).

| Variables | $n$ | $r$ | $P$ |
|---|---|---|---|
| A. Environmental and Geographic | | | |
| Latitude | 46 | −.402 | .001 |
| Longitude | 46 | .598 | <.001 |
| Elevation | 46 | .161 | ns |
| Slope | 92 | .360 | .001 |
| % Clay Content | 92 | .341 | .001 |
| Litter Depth | 92 | .337 | <.001 |
| B. Soil | | | |
| % Humic Matter (by Volume) | 77 | .201 | ns |
| CEC (meq./100 cm³) | 77 | .085 | ns |
| BSP (% of CEC) | 77 | .044 | ns |
| Acidity, (meq./100 cm³) | 77 | −.098 | ns |
| pH | 77 | .097 | ns |
| P−index | 77 | −.335 | .01 |
| K−index | 77 | .131 | ns |
| Ca−% of CEC | 77 | .0002 | ns |
| Mg−% of CEC | 77 | .156 | ns |
| Zn−index | 77 | −.185 | ns |
| Cu−index | 77 | −.306 | .01 |
| C. Morphological | | | |
| Petiole Length | 92 | .077 | ns |
| Leaf Width | 92 | −.180 | ns |
| Leaf Length | 87 | −.173 | ns |
| Capsule Length | 29 | −.373 | .05 |
| Capsule Width | 28 | −.504 | .01 |
| Peduncle Length | 37 | .390 | .05 |
| Rhizome Wet Weight | 92 | .332 | .01 |
| Rhizome Dry Weight | 90 | .123 | ns |
| Rhizome Volume | 92 | .334 | .01 |

and width measurements) were correlated positively and capsule size was correlated negatively with sanguinarine (Table 1C).

A stepwise multiple regression of sanguinarine content with the independent variables revealed only latitude, pH, and soil organic content accounted for significant variation (Table 3). All stepwise procedures selected latitude, pH and percent humic matter constitute as the best three-variable model even though single-variable regressions with each are significant only for latitude (Figure

Table 2. ANOVA table for % sanguinarine in structured and unstructured soils.

| Soil Structure | % Sanguinarine $\bar{x} \pm$ SE ($n$) | F Value | $P$ |
|---|---|---|---|
| Unstructured | 2.33 .188 (44) | 20.58 | .0001 |
| Structured | 3.40 .145 (48) | | |

2). We excluded longitude from the analyses; its significance largely is due to low sanguinarine levels from North Carolina's coastal plain. Seasonal variation is due to higher alkaloid concentrations during flowering and fruiting periods early in the year (Figure 3).

## DISCUSSION

Sanguinarine content is correlated negatively with latitude; highest-yielding populations were from the southern Appalachians and lowest from north of the West Virginia–Pennsylvania border and in North Carolina's coastal plain. Clinal variation, especially along north-south gradients occurs in many secondary metabolites including terpenes (Zavarin et al., 1975, 1978), flavonoids (Nicholls and Bohm, 1982; Levy and Fujii, 1978) and alkaloids (Levin and York, 1978).

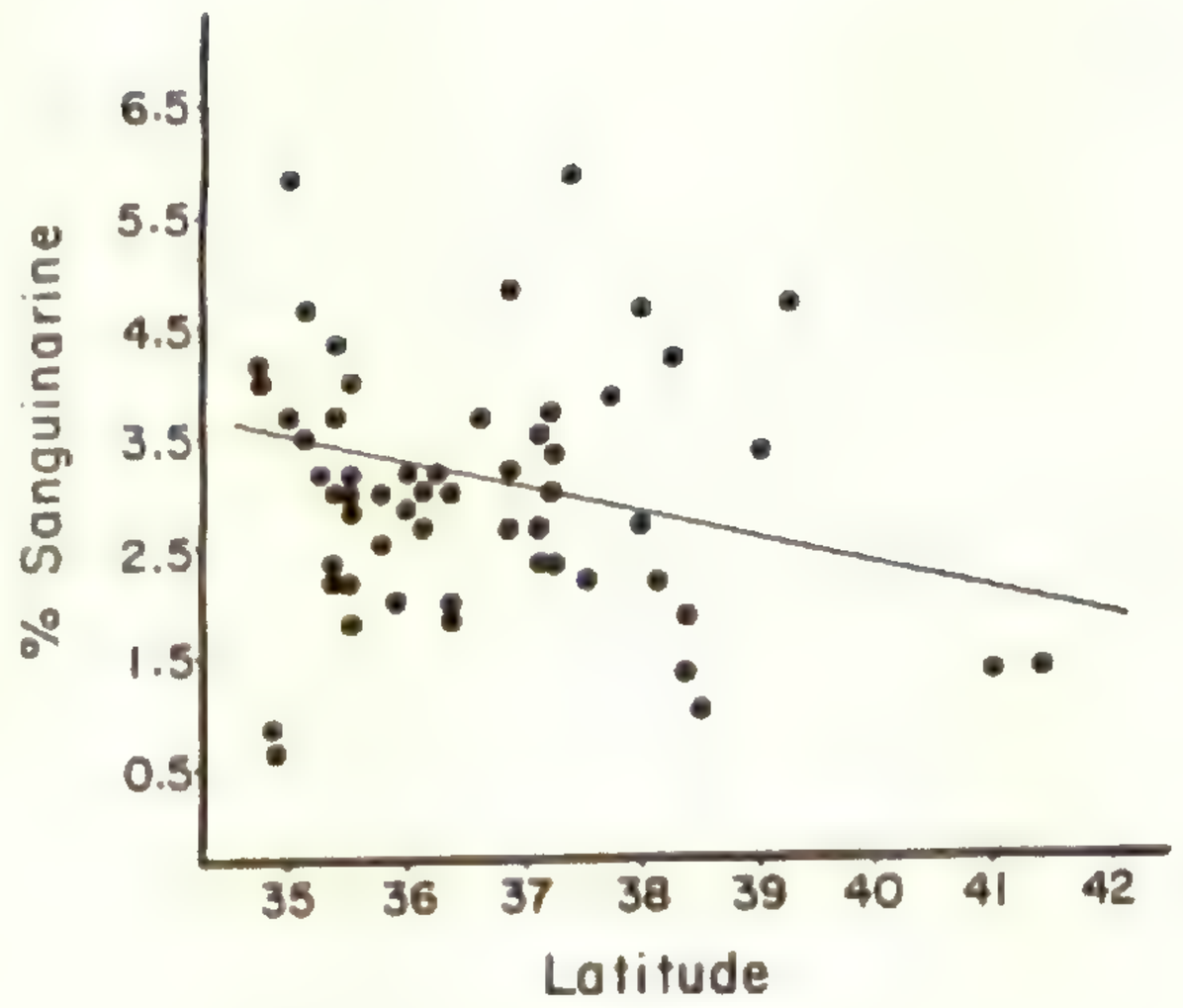
The correlation between sanguinarine content and longitude is spurious. The low-yielding populations in the north were also located farther east than most others. Sanguinarine concentrations peak in mountains or in mountain-like habitats; they are lower in the eastern piedmont and coastal plain in the central valley to the west.

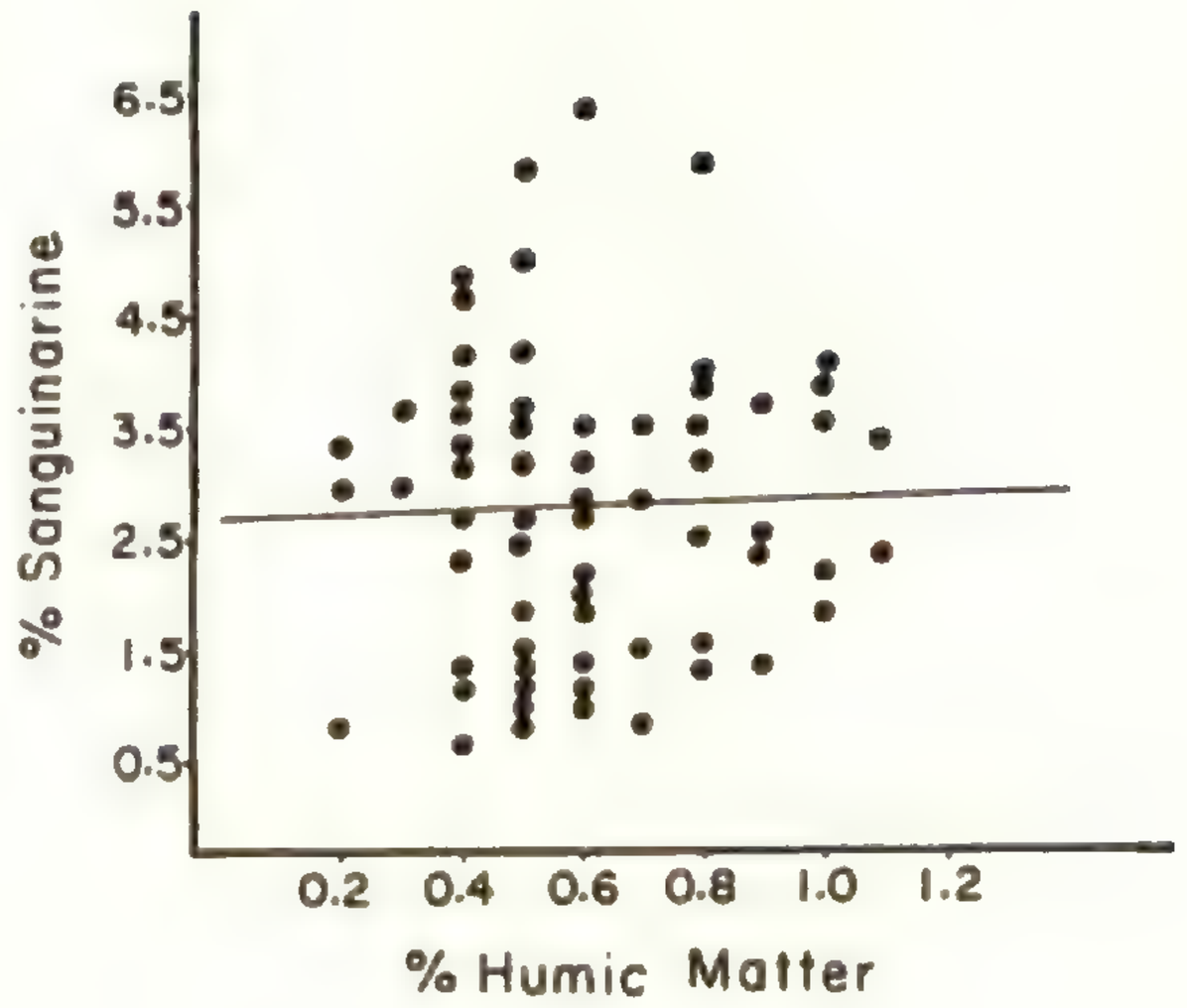
Among the environmental factors positively correlated with sanguinarine concentrations are litter depth, slope, clay content and soil structure. High-yielding populations grew in mature, undisturbed, deciduous forests often dominated by *Liriodendron tulipifera* L. or *Acer saccharum* Marshall and *Fagus grandifolia* Ehrhart. Other factors affecting secondary metabolites include light, pH, moisture, soil chemistry, temperature, altitude, successional status, geographical location, plant tissue, tissue age, cell age, and herbivory (*see* Harborne and Turner, 1984).

Production of secondary compounds varies considerably both within and between plant species. A general consensus is that conditions favoring optimal growth also favor the greatest pro-

Table 3. One, two and three-variable model results of the maximum R-square improvement stepwise regression procedure.

| Variables | One-Variable Model | | | Two-Variable Model | | | Three-Variable Model | | |
|---|---|---|---|---|---|---|---|---|---|
| | B-Value | F | *P* | B-Value | F | *P* | B-Value | F | *P* |
| Intercept | 15.98 | | | 14.02 | | | 11.04 | | |
| Latitude | −.35 | 57.7 | <.001 | −.37 | 74.3 | <.001 | −.35 | 70.4 | <.001 |
| pH | | | | .48 | 13.0 | <.001 | .73 | 24.3 | <.001 |
| % Humic Matter | | | | | | | .80 | 10.14 | .01 |
| R-Square | | .453 | | | .519 | | | .578 | |



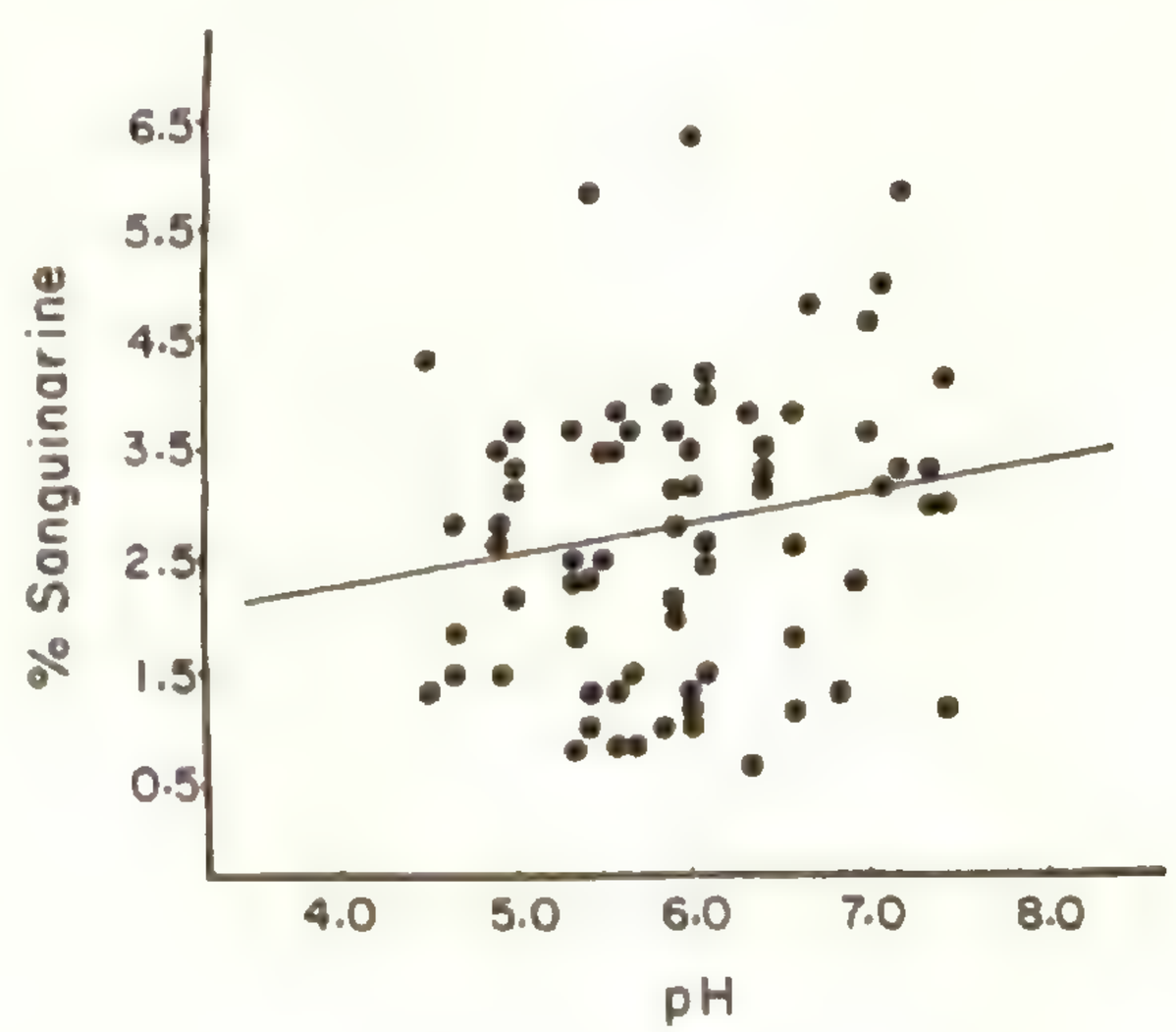




Figure 2. Single variable regressions of sanguinarine concentration and three environmental variables. (a) latitude: $r = -.40$, $P < .001$; (b) pH: $r = .19$, $P < .10$; and (c) % humic matter, $r = .017$, $P = .90$.

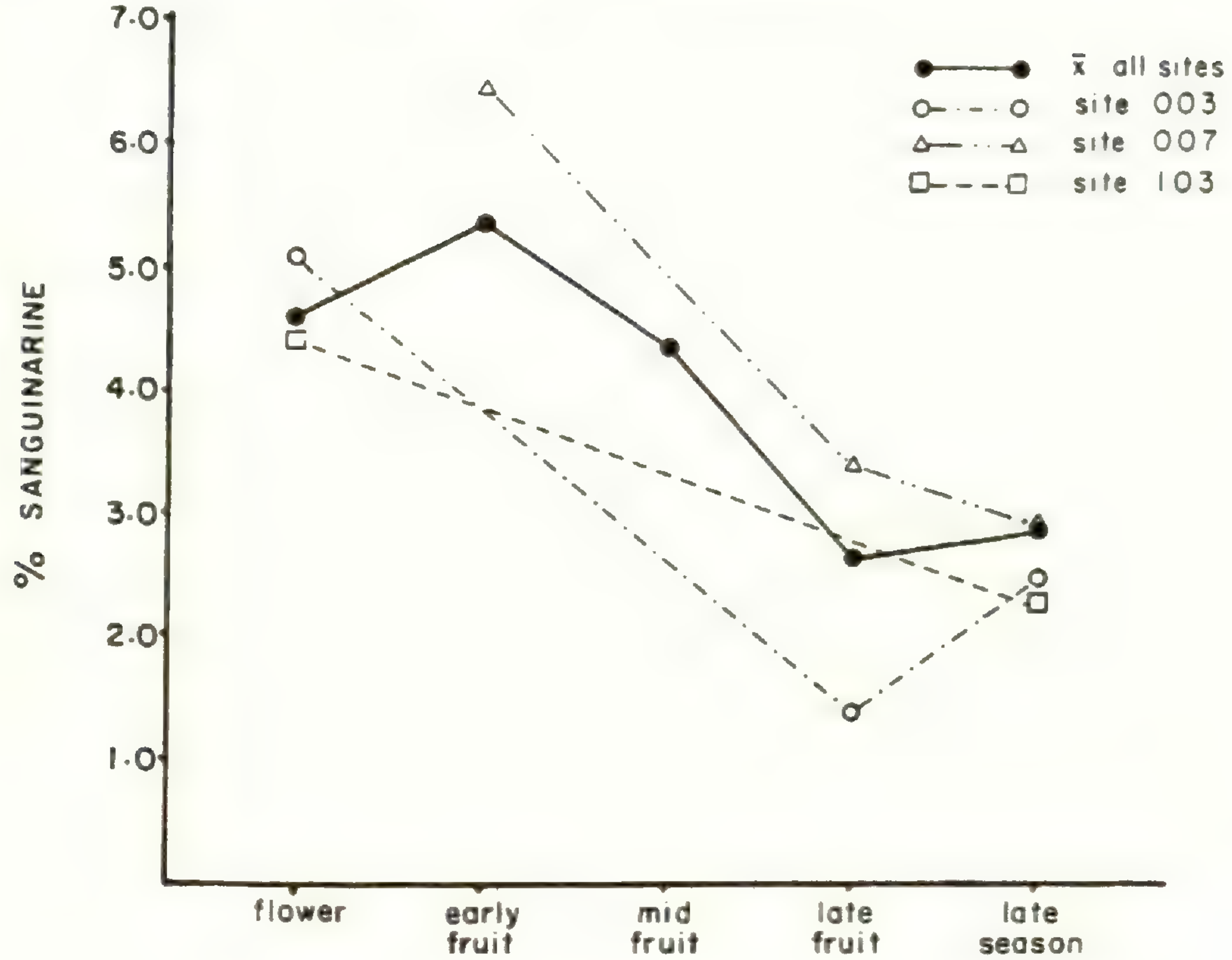



Figure 3. Seasonal variation of rhizome sanguinarine content in *Sanguinaria canadensis.*

duction of secondary metabolites. Levin (1976) suggested that optimal growth conditions for a species create optimal conditions for its predators and pathogens. If this connection is true, then selection should favor greater production of protective compounds in such habitats. *Sanguinaria* grows best in cool, shaded, forest understories on circumbasic soils. We usually found higher alkaloid concentrations in these habitats. Nevertheless, we found one of the highest sanguinarine concentrations in a small, exposed population growing under marginal conditions.

The correlation between rhizome weight or volume and sanguinarine content suggests a net accumulation of the alkaloid with time. Alkaloid concentrations are a function of synthesis, degradation, and translocation rates. In rhizomes, these processes occur over the life of the plant, in leaves they occur in a single season. We found foliage levels of .5% sanguinarine but Hegnauer (cited in Levin and York, 1978) reported levels of .08%. Cates and Rhoades (1977) noted that toxins, including alkaloids, are

usually characteristic of ephemeral tissues and that concentrations decrease rapidly in longer-lived plant tissues. This finding is not so for bloodroot.

The allocation of protective compounds in *Sanguinaria* is also counter to other hypotheses of plant defense. Feeny (1976) and Rhoades and Cates (1976) suggested that alkaloids should be found in "unapparent plants" (in Feeny's terminology) or those of young successional stages. These species can potentially escape from predators in both space and time. On the other hand, "apparent plants," characteristic of mature communities, should be defended by substances that reduce digestibility (e.g., tannins) and are metabolically more costly. Perennial herbs should have intermediate strategies according to Rhoades and Cates (1976). *Sanguinaria canadensis* has foliage-defense allocations characteristic of "unapparent plants" to their potential predators, soil-borne pathogens. Although rhizomes contain high levels of secondary metabolites, these products are toxic alkaloids which should be characteristic of "unapparent plants."

The high sanguinarine concentration in bloodroot rhizomes is an anomaly, especially considering the alkaloid's toxicity to soil pathogens at very low concentrations (Greathouse, 1939). Cates and Rhoades (1977) noted that toxins are often found in small quantities, sometimes less than 2% by dry weight. Levin and York (1978) found that alkaloids made up an average of .62% dry weight of leaf tissues in plants with these compounds. We found similar foliage concentrations in *Sanguinaria* but considerably more in rhizomes. Allelochemical effects of the water-soluble sanguinarine are unknown.

Leaf width, length, and petiole length were not significantly correlated with sanguinarine content, perhaps because alkaloid content of rhizomes is a function of several years of accumulation and does not necessarily represent present conditions. On the other hand, capsule length and width were positively correlated with sanguinarine levels. Both are measures of reproductive effort. Harris (1910) found that seed and ovule number per fruit and fruit length were significantly correlated. The negative relation between capsule length and alkaloid concentration may represent an energy tradeoff between reproduction and defense.

Seasonal variation in secondary metabolite concentrations occur in *Pteridium aquilinum* (L.) Kuhn flavonoids (Cooper-Driver et al., 1977), *Dentaria* spp. glucosinolates (Feeny and Rosenberry,

1982) and *Chelidonium majus* L. alkaloids (Kustrak et al., 1982). Our preliminary data show that rhizome sanguinarine concentrations peak early then decrease continually through the season. A similar pattern occurs in *P. aquilinum* flavonoids (Cooper-Driver et al., 1977) and some *Sanguinaria* populations (Farwell, 1915; Homerberg and Beringer, 1913). The two latter papers refuted a suggestion in the U.S. Pharmacopeia that *Sanguinaria* should be harvested just before leaf senescence for maximum alkaloid yield.

Some plants translocate alkaloids into above-ground tissue very early in the season. This translocation may be a cause of seasonal variation. Alternatively, the continuous decrease in concentration through the season may simply result from carbohydrate accumulation at a greater rate than alkaloid synthesis. Our data suggest that older bloodroot rhizomes have higher alkaloid concentrations than younger ones so that there must be a net accumulation each year. In contrast to *Sanguinaria* alkaloid concentrations in *Chelidonium majus,* a closely related member of the Papaveraceae, show the opposite seasonal trend (Kustrak et al., 1982).

If alkaloids are metabolically expensive to produce, then allocation to different tissues should be influenced by selection. The greater allocation to the perennial rhizome than to the ephemeral above-ground tissue should increase fitness. As a corollary of Levin's (1976) pest-pressure hypothesis, we suggest that increasing pest, predator, or disease pressure along a north-south gradient in the southern Appalachians may be responsible for higher alkaloid concentrations within southern bloodroot populations. We know of no data to refute or corroborate this hypothesis at present. Within a geographic region, however, high alkaloid concentration occur under optimal growth conditions for *Sanguinaria.*

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# ACHENE MICROMORPHOLOGY OF THE *CAREX NIGROMARGINATA* COMPLEX (SECTION *ACROCYSTIS*, CYPERACEAE)

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## ABSTRACT

Principal component and cluster analyses, in addition to individual achene micromorphological characters, divide the *Carex nigromarginata* complex into two groups: achenes of *C. nigromarginata, C. floridana* and *C. peckii* have cell central bodies with concave sides while the remaining three taxa have cell central bodies with convex sides. This evidence supports the reduction of *C. artitecta* and *C. physorhyncha* to varieties of *C. emmonsii* (as *C. emmonsii* var. *muhlenbergii, C. emmonsii* var. *australis* and *C. emmonsii* var. *emmonsii,* respectively). The six taxa can only be distinguished by significant differences between the achene characters; achene micromorphological data are most useful in dividing the complex into sets of taxa.

Key Words: *Carex, Carex nigromarginata, Acrocystis, Montanae,* Cyperaceae, micromorphology, SEM, Angiosperm systematics, eastern North America

## INTRODUCTION

The *Carex nigromarginata* Schwein. complex consists of six closely related taxa within section *Acrocystis* Dumort. (= *Montanae* (Fries) Carey). Mackenzie (1935) treated these taxa as six distinct species: *C. nigromarginata, C. floridana* Schwein., *C. peckii* Howe ex Peck, *C. emmonsii* Dewey ex Torrey (as *C. albicans* Willd. ex Sprengel), *C. artitecta* Mackenzie and *C. physorhyncha* Liebm. ex Steudel. Radford et al. (1968) and Lahham (1980, Ph.D. dissertation, Penn. State Univ.), however, included *C. floridana* as a variety of *C. nigromarginata.* Gleason and Cronquist (1963) and Scoggan (1978) treated *C. peckii, C. emmonsii* and *C. artitecta* as varieties of *C. nigromarginata.* Voss (1972) indicated that *C. artitecta and C. emmonsii* are "distinguished only with great difficulty."

The above treatments were all essentially macromorphological in nature and other types of data have been employed in other groups of *Carex* to help clarify both infra- and interspecific re-

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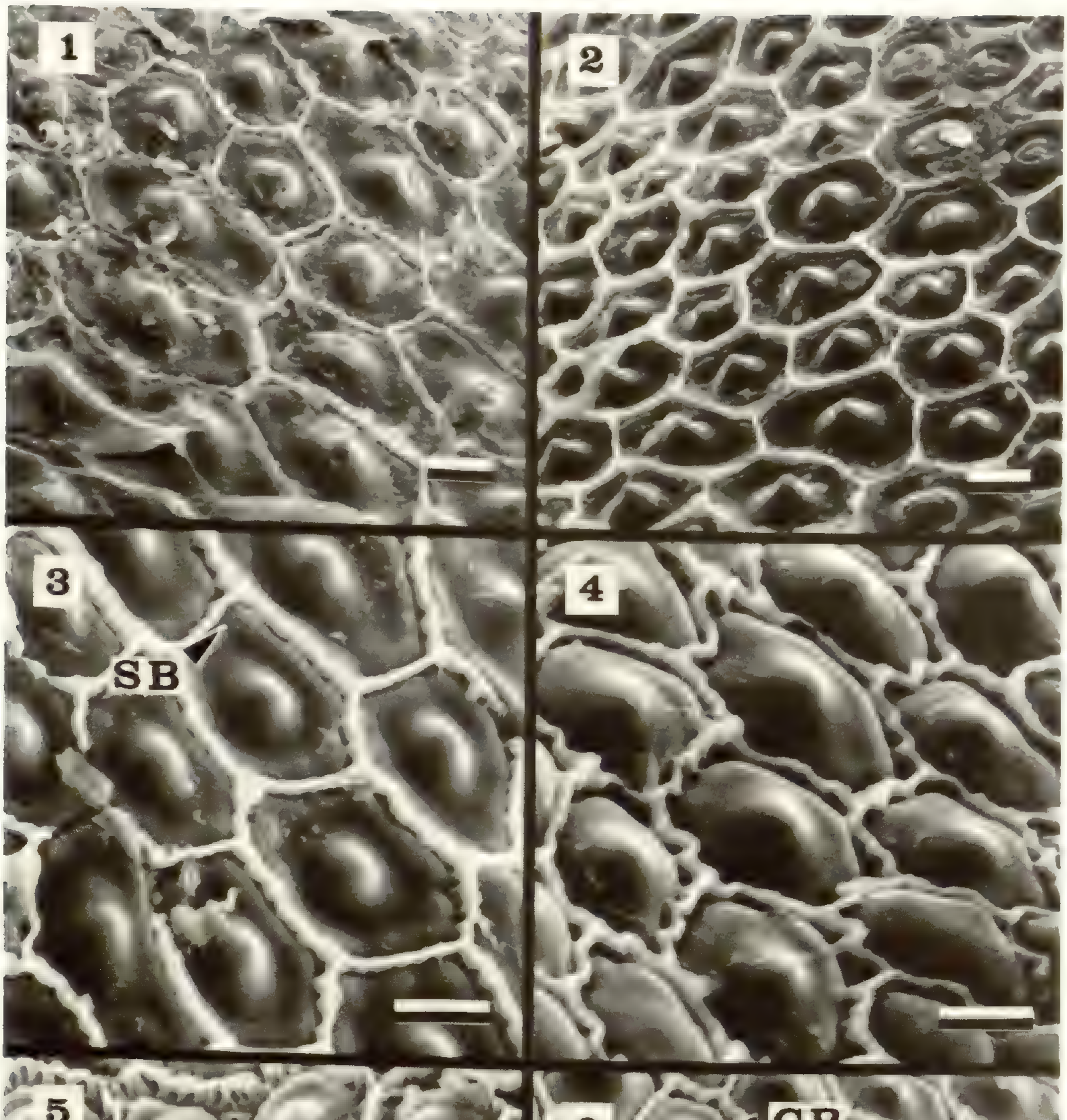
lationships. Other types of data also have been helpful within this complex. Rettig (1988, Ph.D. dissertation, Univ. Georgia, Athens; 1989) treated *C. artitecta* and *C. physorhyncha* as varieties of *C. emmonsii* (*C. emmonsii* var. *muhlenbergii* (A. Gray) J. Rettig and *C. emmonsii* var. *australis* (L. Bailey) J. Rettig, respectively) based on phenetic analyses of macromorphological data, flavonoids and achene micromorphology.

Achene micromorphology has proved taxonomically useful in numerous species groups in *Carex* (e.g., Walter, 1975; Toivonen and Timonen, 1976; Timonen and Toivonen, 1979; Toivonen, 1980; Hoshino, 1984; Menapace and Wujek, 1985; Standley, 1985, 1986, 1987a, 1987b; Wujek and Menapace, 1986; Bruederle et al., 1989). Selected micromorphological characters have also been studied in some North American members of section *Acrocystis*. Lahham (1980, op. cit.) investigated epidermal peels, internal anatomy of culms and leaf blades, and surfaces of pollen grains and achenes. Of these characters, Lahham concluded that only achene surfaces were useful in distinguishing taxa.

Most of the above studies have been subjective comparisons of achenes between taxa. Menapace et al. (1986) and Menapace and Wujek (1987) made the first attempts at an objective approach to examining the surface features of *Carex* achenes. In each study, a data matrix and phenogram was constructed by scoring micrographs with characters that "could be scored more or less unequivocally for each species" (Menapace et al., 1986). Preliminary examination of achene micrographs within the *C. nigromarginata* complex (Figures 1–6) revealed that variation between the achenes of a single taxon and even among the cells of a single achene would make it difficult to unequivocally assign a character state to a taxon or even to a single achene. An attempt was made to overcome this problem by utilizing a method that does not require the entire taxon to be scored unequivocally. Variation within a taxon was taken into account by scoring characters on randomly chosen cells on a single achene.

## METHODS AND MATERIALS

Plant materials used are cited in Table 1. Specimens from each taxon were selected to represent a wide range of geographical and macromorphological variation. Achenes were treated with acetic acid for 24 hr., placed in a bath-type ultrasonic cleaner for up to




Figures 1–6. Representative scanning electron micrographs of the achene surface in the *Carex nigromarginata* complex. **1.** *C. nigromarginata* (*Rettig 1430*). **2.** *C. floridana* (*Rettig 1514*). **3.** *C. peckii* (*Cody 6930*). **4.** *C. emmonsii* var. *emmonsii* (*Rettig 1030*). **5.** *C. emmonsii* var. *muhlenbergii* (*Morton 7132*). **6.** *C. emmonsii* var. *australis* (*Rettig 1525*). CB = central body, HW = honeycombed anticlinal wall, SB = satellite body, SW = sinuous anticlinal wall. Scale bars = 10 μ.

Table 1. Origin and accession number of collections of the *Carex nigromarginata* complex sampled.

*Carex nigromarginata.* **Alabama:** Tuscaloosa Co., *Rettig 1447* (GA). **Georgia:** Hancock Co., *Rettig 1430* (GA); Habersham Co., *Manhart 212* (GA); Union Co., *Rettig 1456* (GA).

*Carex floridana.* **North Carolina:** Bladen Co., *Rettig 1514* (GA); Brunswick Co., *Godfrey 49005* (GA).

*Carex peckii.* **New York:** Essex Co., *House 8059* (NY). CANADA. **Alberta:** *Cody 6930* (GH). **British Columbia:** *Calder 17030* (GA).

*Carex emmonsii* var. *emmonsii.* **North Carolina:** Madison Co., *Rettig 1030* (GA). **Pennsylvania**: Centre Co., *Wahl 977* (GH); Tioga Co., *Rettig 1330* (GA); Warren Co., *Rettig 1343* (GA). **Tennessee:** Johnson Co., *Rettig 1538* (GA). **Virginia:** James City Co., *Rettig 1530* (GA).

*Carex emmonsii* var. *muhlenbergii.* **Arkansas:** Polk Co., *Rettig 1483* (GA); Pope Co., *Rettig 1490* (GA). **New Jersey:** Warren Co., *Morton 7132* (NY). **North Carolina:** Transylvania Co., *Rettig 1555* (GA).

*Carex emmonsii* var. *australis.* **Alabama:** Henry Co., *Rettig 1440* (GA); Marshal Co., *Kral 34196* (GA). **Arkansas:** St. Francis Co., *Rettig 1497* (GA). **Florida:** Liberty Co., *Rettig 1224* (GA). **Mississippi:** Calhoun Co., *Rettig 1452* (GA); Washington Co., *Rettig 1455* (GA). **Texas:** Shelby Co., *Rettig 1459* (GA). **Virginia:** Brunswick Co., *Rettig 1526* (GA). MEXICO. **Chapingo:** *Koch 7827* (MO).

2 hr. or a probe-type sonifier for up to 15 min. to remove the outer periclinal wall, air-dried and then sputter-coated in a Hummer V Sputter Coater to give a coating of approximately 20 $\mu$ in thickness. Upper shoulders of achenes were photographed using a JOEL scanning electron microscope at an accelerating voltage of 15 kV.

A data matrix was constructed using 10 characters (8 binary, 2 quantitative) that could be scored for each cell on every achene (Table 2). Five randomly chosen cells were scored for each achene and means ($\bar{Y}$) were then calculated to give a single score for each character for every achene. To identify characters contributing most to differences between taxa, a principal component (PC) analysis was performed using standardized data (Sneath and Sokal, 1973), and a correlation matrix was generated to determine which characters were significantly correlated with the PC's. General linear modeling was performed to determine which characters were significantly different between the taxa. Standardized data were used to calculate pair-wise similarity-dissimilarity matrices using euclidian distances, and phenograms were prepared using average linkage clustering (UPGMA). Alpha level for all statistical procedures was .05 unless otherwise specified. Cluster analysis

Table 2. Characters used in the achene micromorphological phenetic analysis.

| Acronym | Derivation |
|---|---|
| APEX | Apex shape of central body—rounded vs. pointed |
| APPRESS | Margins of platform appressed to platforms of adjacent cells (Figure 2)—vs. nonappressed (Figure 4) |
| CBSIDE | Sides of central body/platform—convex vs. concave (sunken below surface) |
| CENBOD | Central body (bump on top of platform)—present or absent |
| LENGTH | Maximum length of cell at widest point |
| NUMWALL | Number of anticlinal walls |
| PLATFM | Corners of platform (raised portion of central portion of cell)—round vs. angular |
| SATBOD | Satellite bodies (raised bumps) at margins of platform—present (Figure 3) or absent |
| SHPWALL | Shape of anticlinal walls—curved vs. linear |
| TYPWALL | Type of anticlinal walls—solid vs. honeycombed (Figure 5) or sinuous (Figure 6) |

was performed via SPSS/PC+ (Norusis, 1986); other analyses were performed with SAS Version 6 (1987).

## RESULTS AND DISCUSSION

Representative scanning electron micrographs of the six taxa in the complex are shown in Figures 1–6. Figure 1 shows the outer periclinal wall partially removed to expose the diagnostic features of the surface. The complex in general is characterized by fewer diagnostic characters than are used to distinguish some other species of *Carex* (e.g., Hoshino, 1984).

The complex can be divided into two groups based on the shapes of the sides of the central body/platforms. This character (CBSIDE) is constant for all cells of all achenes of all taxa examined. Achenes of *Carex nigromarginata, C. floridana* and *C. peckii* (Figures 1–3) are characterized by a central body with concave sides compared to a central body with convex sides in *C. emmonsii* s.l. (Figures 4–6).

This division of the complex into two groups is supported by multivariate analyses of the characters. A plot of the first two PC's (accounting for 37.1% and 17.3% of the variation, respectively) also divides the complex into two sets of taxa: *Carex nigromarginata, C. floridana* and *C. peckii* on the positive end of

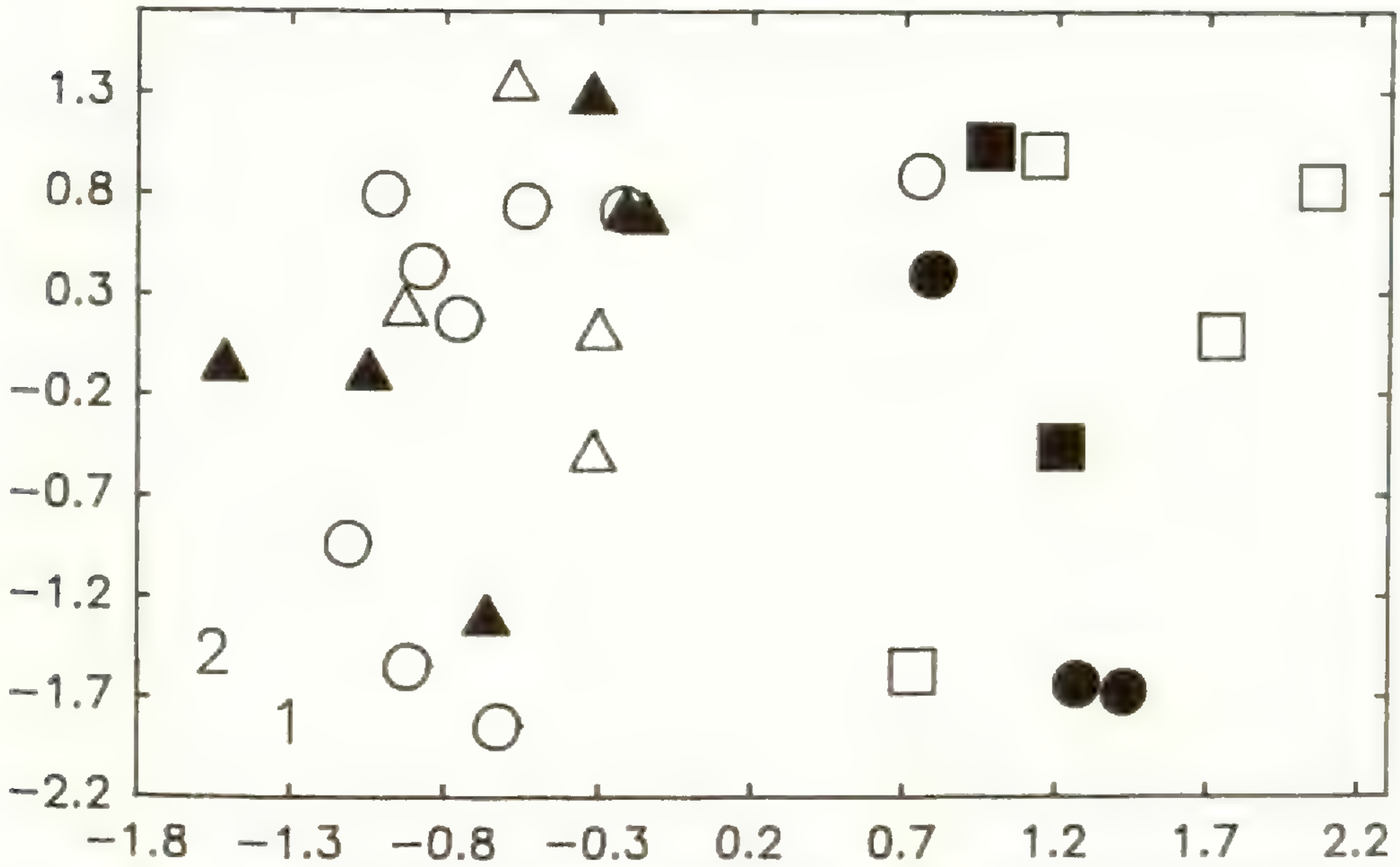



Figure 7. Principal component ordination of the *Carex nigromarginata* complex specimens. *C. nigromarginata* (■); *C. floridana* (□); *C. peckii* (●); *C. emmonsii* var. *emmonsii* (▲); *C. emmonsii* var. *muhlenbergii* (△); *C. emmonsii* var. *australis* (○). Characters correlated ($P < .001$) to the PC's were (acronyms according to Table 2): PC1—CBSIDE, APPRESS, PLATFM, SATBOD, and LENGTH; PC2—NUMWALL and SHPWALL.

PC1 and *C. emmonsii* s.l. toward the negative end (Figure 7). Only one specimen of *C. emmonsii* var. *australis* (*Koch 7827*) is not grouped with the other specimens of *C. emmonsii* s.l. possibly due to the presence of satellite bodies on some cells. *Koch 7827* is correctly identified based on macromorphological characters. Cluster analysis (Figure 8) using the qualitative characters also divides the complex into two sets of specimens: the upper cluster contains all of the specimens of *C. nigromarginata, C. floridana* and *C. peckii*; the lower cluster contains all specimens of *C. emmonsii* s.l., including *Koch 7827*.

Segregation of the complex into two subgroups is supported by macromorphological data. Principal component, cluster and discriminant function analyses of 26 macromorphological characters also divide the complex into two sets of taxa corresponding to *C. emmonsii* s.l. and the three remaining taxa (Rettig, 1988, op. cit.). Two of these macromorphological characters (achene body length and perigynium width) also divide the complex into two sets of taxa. Additional evidence comes from flavonoid data: *C. emmonsii* s.l. lacks tricin compounds present in the remaining taxa

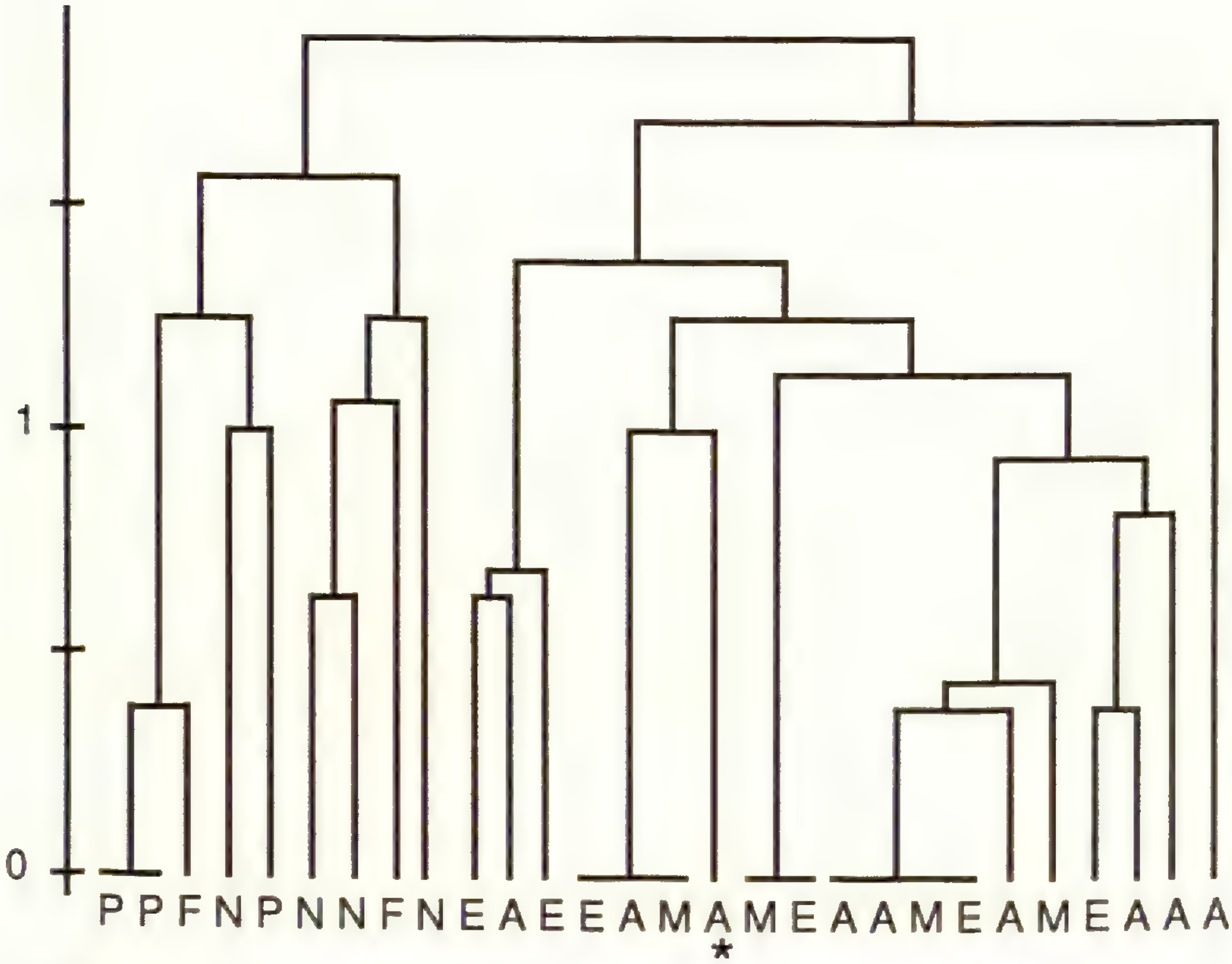



Figure 8. Phenogram for the *Carex nigromarginata* complex specimens using average linkage (UPGMA) with selected characters. Scale indicates euclidean distance. Asterisk = *Koch 7827*. N = *C. nigromarginata*, F = *C. floridana*, P = *C. peckii*, E = *C. emmonsii* var. *emmonsii*, M = *C. emmonsii* var. *muhlenbergii*, A = *C. emmonsii* var. *australis*.

and an unidentified compound is present in *C. emmonsii* s.l. but absent from the other taxa (Rettig and Giannasi, unpubl. data).

Neither PC nor cluster analyses of the achene micromorphological characters further divides the complex into discrete taxa which correspond to the macromorphology. Lack of separation could be due in part to the paucity of ornamentation and scoreable characters that can be used in the analyses or the variable nature of the achene surface. Most of the specimens cannot be assigned to a taxon based solely on examination of its micrograph, and thus it appears that the micromorphology of this complex may not be as useful at the interspecific level as has proven in other groups. However, an advantage of scoring characters on individual cells of an achene is that the data can be used to separate the taxa based on significant differences of the characters.

*Carex nigromarginata* (Figure 1) and *C. floridana* (Figure 2), which differ from each other in two characters (APPRESS,

PLATFM), significantly differ from the other four taxa by having central bodies of adjacent cells appressed. *Carex peckii* (Figure 3) can be distinguished from the other taxa (with the exception of *C. nigromarginata*) by having a significantly greater number of cells with satellite bodies around the central body. *Carex peckii* differs from *C. nigromarginata* in one character (PLATFM).

There is no single character that is constant in all cells of all achenes examined that can be used to distinguish the three varieties of *Carex emmonsii* s.l. (Figures 4–6). Therefore, a given specimen cannot be assigned to one of these three taxa with any degree of certainty. However, *C. emmonsii* var. *muhlenbergii* is significantly different from *C. emmonsii* var. *australis* based on the presence of a central body (*C. emmonsii* var. *muhlenbergii* always has one present, while some achenes of *C. emmonsii* var. *australis* usually have cells that lack a central body). *Carex emmonsii* var. *emmonsii* is significantly different from *C. emmonsii* var. *muhlenbergii* in the sinuous nature of the anticlinal walls. Anticlinal walls of *C. emmonsii* var. *muhlenbergii* are always sinuous while the achenes of *C. emmonsii* var. *emmonsii* usually have non-sinuous anticlinal walls.

Achene micromorphological data do not support the taxonomic conclusions of some previous authors. Both *Carex emmonsii* s. str. and *C. emmonsii* var. *muhlenbergii* have been treated as varieties of *C. nigromarginata*. The data presented here suggest that these two taxa, along with *C. emmonsii* var. *australis*, form a distinct set of taxa more closely related to each other than to *C. nigromarginata*.

*Carex peckii* and *C. floridana* also have been treated as varieties of *C. nigromarginata*. However, achene micromorphology suggests that both are distinct species. *Carex peckii* appears to be the most distinct taxon within the complex because of a unique combination of the presence of sinuous anticlinal walls and prominent satellite bodies. *Carex peckii* also appears to be the most derived taxon within this complex based on flavonoid chemistry (Rettig and Giannasi, unpubl. data). The species is characterized by a general loss of several flavones but has an increase in the diversity of remaining C-glycosylflavones. These trends are paralleled by the increased prominence of the satellite bodies on the achene surface which are more developed than those found in *C. nigromarginata*. Crins and Ball (1988) concluded that "increasing distinct satellite bodies" were a derived condition in sect. *Cerato-*

*cystis* Dumort. and correlated with trends in cytology, ecology, chemistry, achene shape, spike morphology and features of the perigynium epidermis. These correlations do not seem to occur within the *C. nigromarginata* complex as a whole. *Carex floridana* also appears to be more derived than *C. nigromarginata* based on flavonoid chemistry (Rettig, 1988, op. cit.; Rettig and Giannasi, unpubl. data) but achenes of *C. floridana* do not possess the number or development of satellite bodies of either *C. nigromarginata* or *C. peckii.*

In conclusion, achene micromorphological data provide some evidence for recognition of six distinct taxa within the *Carex nigromarginata* complex based on significance differences in the individual characters. The major value of this approach is that multivariate analysis of these characters on each achene divided the complex into two sets of taxa providing information on relationships within the complex that would otherwise not be apparent.

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# RANGE EXPANSIONS OF SOME GRASSES IN VERMONT

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## ABSTRACT

Distribution data are updated for 14 Poaceae taxa considered rare in Vermont 20 years ago. Two of the natives studied, *Glyceria acutiflora* and *Sporobolus asper,* are still rare, have lost historical populations, and face potential human alteration of their habitats. They are recommended for Endangered species status in Vermont. Six native species have expanded their range north. Seven native species are now weedy in disturbed habitats. Railroads and roadsides provide habitat and a means of dispersal for the weedy species. *Aristida basiramea* and *Diplachne acuminata* are novelties in the Vermont flora.

Key Words: endangered species, grasses, range extensions, rare species, Vermont flora, weeds

Distributions of Vermont's grasses were well documented between the 1870's and the 1930's. Since then, only Frank Seymour seriously collected or wrote about Vermont's grasses. Many grasses expanded their ranges since Seymour's 1969 *Flora of Vermont* was published. For example, *Puccinellia distans* (L.) Parl. increased dramatically in Vermont since it was initially discovered in 1966 (Seymour, 1967; Zika, 1988). This finding prompted a study of the changing distributions of 14 grass taxa considered rare in Vermont 15 years ago. Rarity was defined as known from three or fewer historical sites. In addition, this study investigated the suggestion by Countryman (1978) that many of the supposedly rare grasses in Vermont might simply have been overlooked by recent collectors.

The historical sites were visited, where possible, and many new sites were field-checked where the habitat seemed suitable for one or more of the taxa. Herbarium vouchers were deposited at VT unless otherwise noted.

## DISTRIBUTION DATA

### Aristida basiramea

*Aristida basiramea* Engelm., a midwestern species, was first collected in Vermont in 1975 in a railroad yard in White River Junction, Windsor Co. (*Sundell 1308* HNH). It is now a dominant grass at Sundell's station. Recent Vermont records are largely

from railroad right-of-ways: Chittenden Co., Burlington 1981, Milton (sandy field) 1983; Franklin Co., St. Albans 1981; Washington Co., Montpelier Junction (Berlin) 1981, Waterbury 1981; Windham Co., Bellows Falls (Rockingham) 1981; and Windsor Co., White River Junction (Hartford) 1981. The Burlington station apparently was not present in 1975, when the late Harry E. Ahles collected there and recorded two other *Aristida* species (Zika et al., 1983).

*Aristida basiramea*'s range expansion is not unique to Vermont. Smith (1965) noted it increased in northern New York state after 1924. Pease (1964) recorded it from five towns in northern New Hampshire, after first collecting it in 1954. In Maine *A. basiramea* was known from only Oxford Co. (Richards et al., 1983), where since 1938 it spread from two to seven towns (Campbell and Eastman, 1980). Two Canadian stations were located relatively recently in Ontario (Dore and McNeill, 1980).

**Aristida dichotoma**

Recent field work failed to re-locate historical populations of *Aristida dichotoma* Michx. reported by Seymour (1982) in Pownal (1904) and New Haven (1878–96); these populations are assumed extirpated. A station reported in Essex by Flynn (1911) is based on *Sporobolus neglectus* Nash (*Flynn s.n.* TUFT). In 1977, Ladd (1979, unpubl. M.S. thesis, S. Ill. U., Carbondale) located an adventive *Aristida dichotoma* colony in the Montpelier Junction railroad yard, while cataloging the flora of Washington Co.

Recent Vermont records of poverty-grass are mostly from train stations: Chittenden Co., Burlington 1981; Franklin Co., St. Albans 1981; Washington Co., Montpelier Junction 1977, 1981, Waterbury 1981; Windham Co., Bellows Falls 1981, Brattleboro 1981, Jamaica (sandy roadside) 1981, South Vernon 1984, Vernon (sandy quarry) 1982; Windsor Co., White River Junction 1981, and Windsor 1981.

The Burlington population apparently was not extant in 1975, when Ahles collected at the site and recorded two other *Aristida* species (Zika et al., 1983).

**Aristida oligantha**

*Aristida oligantha* Michx., is common on railroad lines where it is indigenous in the midwest (e.g., Muhlenbach, 1979). It ap-

parently disperses well as an adventive along railroads in the northeast. The first Canadian record (Catling et al., 1978) and the first New Hampshire record (1977 *Ahles 84918* MASS, NHA) are from train tracks. Ahles discovered the taxon in Vermont in 1975, in Burlington, Chittenden Co. (Zika et al., 1983). It is now abundant at the original collection site, a railroad yard on the shore of Lake Champlain. In 1981, *A. oligantha* was collected along railroads in: Franklin Co., St. Albans; Windham Co., Bellows Falls, Brattleboro; Windsor Co., White River Junction, and Windsor.

**Diplachne acuminata**

*Diplachne acuminata* Nash [= *Leptochloa fascicularis* (Lam.) A. Gray var. *acuminata* (Nash) Mohlenbrock], sprangletop, is a new genus and species in the flora of Vermont. This Eurasian adventive is expanding its range north and east (McNeill, 1979). It first reached southern Canada in 1976, on a railroad near Niagara Falls (Catling et al., 1978). The first Massachusetts collection was in 1979. The first Vermont collection was in 1981, at a damp siding in the railroad yard on Lake Champlain in Burlington, Chittenden Co. (*Zika 4952* VT, *5249* NEBC, VT). The colony consisted of circa 200 stems in 1985.

**Eragrostis capillaris**

Countryman (1978) included *Eragrostis capillaris* (L.) Nees, lacegrass, on the state Rare and Endangered species list. Native Rutland Co. populations from calcareous ledges were documented in West Rutland 1909 (Kirk, 1910), West Haven 1937, and Castleton 1980. Adventive populations on railroad tracks were collected in Chittenden Co., Burlington 1975, 1980; Franklin Co., St. Albans 1981; Washington Co., Waterbury 1981; and Windham Co., Brattleboro 1981. The weedy colonies are large. This indigenous species is increasing and does not appear to need legislative protection at this time in Vermont.

**Eragrostis frankii**

*Eragrostis frankii* C. A. Mey. ex Steud., also known as lacegrass, is an indigenous species. It was recorded from the shore of the

Connecticut River in the towns of Westminster (1931) and Sharon (1941) when Seymour (1969) wrote his Vermont flora. Countryman (1978) included the species as Rare and Endangered in Vermont. Native colonies on silty shores were recently documented in Addison Co., Ferrisburg 1970; Chittenden Co., Colchester 1983; Orange Co., Braintree 1972; and Windham Co., Vernon 1982. In addition, weedy populations on roadsides were recorded in Bennington Co., East Dorset 1979, and Pownal 1982.

Canadian botanists consider all their *Eragrostis frankii* populations adventive (Dore and McNeill, 1980). With the recent establishment of weedy colonies in Vermont, and an increasing number of native populations, there is no reason to place *Eragrostis frankii* on Vermont's Rare or Endangered species lists.

**Glyceria acutiflora**

*Glyceria acutiflora* Torr., manna grass, a native wetland species, was discovered in Vermont in 1910 in Rutland, Rutland Co. (Kirk, 1911). Kirk's station was never re-located and is assumed extirpated by urban expansion. In 1983 a new station of circa 400 culms was found on the margins of a small pond on Austin Hill, West Haven, Rutland Co. (*Zika 7371* VT). The *Glyceria acutiflora* habitat could be altered by succession or by human disturbance. This strongly suggests that the species warrants listing as a state Endangered species (10 V. S. A., Chapter 123).

**Leptoloma cognatum**

*Leptoloma cognatum* (Schultes) Chase [= *Digitaria cognatum* (Schultes) Pilger], fall witch-grass, is a native perennial frequently growing with two superficially similar taxa: *Panicum capillare* L. and/or *Eragrostis spectabilis* (Pursh) Steudel. All have red to purplish diffuse panicles, and are common on sunny sandy soils. Since there were few historical records, *Leptoloma* was placed on the Vermont Rare and Endangered list (Countryman, 1978).

Wheeler (1912) collected *Leptoloma* in Townshend in 1911, but did not record it elsewhere in the West River Valley. Underwood (1913) documented *Leptoloma* in Hartland in 1912. Kittredge collected it in nearby West Hartford in 1922. She noted it as "rare" in her Woodstock flora (Kittredge, 1939). Apparently *Leptoloma* increased quickly around Woodstock between the time

Kittredge prepared her manuscript and the time it went to press. For in 1939, Kittredge made a Woodstock *Leptoloma* collection (*Kittredge s.n.* HNH) labeled "rare in New England, abundant in Woodstock."

H. E. Ahles (pers. comm.) pointed out that *Leptoloma* is weedy in Vermont, and does not need legal protection. Over the last 15 years, *L. cognatum* increased dramatically in the lowlands of the Connecticut River, West River and in the sand plains of Chittenden Co. Fall witch-grass has also become common in the White River Valley since 1940.

Recent Vermont records are: Chittenden Co., Burlington-South Burlington town line 1981, Colchester 1981, Essex 1982, South Burlington 1975, 1981; Orange Co., Bradford 1983 observation, Fairlee 1983 observation, Thetford 1983; Rutland Co., Rutland 1983 observation; Windham Co., Brattleboro 1982, Dummerston 1981, Jamaica 1981, North Westminster 1981, Putney 1981, Rockingham 1981, Townshend 1911, 1981, Vernon 1982, Westminster 1981; Windsor Co., Hartford 1983, Hartford-Hartland town line 1981, Hartland 1981, Sharon 1983, Springfield 1973, 1981, and White River Junction 1981.

*Leptoloma* recently arrived in southern Canada. It is increasing there (Dore and McNeill, 1980), and along the Connecticut and Merrimac Rivers in New Hampshire.

**Panicum dichotomiflorum**

*Panicum dichotomiflorum* Michx., smooth panic grass, is a new world native. It was first reported in Vermont in 1968 (Seymour, 1970) as an adventive at a construction site in Burlington. H. E. Ahles collected it in Brattleboro in 1978, and D. M. Ladd reported it from Waterbury (1979, unpubl. M.S. thesis, S. Ill. U., Carbondale) on a sandy river bar. *P. dichotomiflorum* is a pesky annual weed that, in 20 years, successfully invaded many disturbed habitats, including roadsides, sidewalks, railroad yards, waste lots, and cultivated fields. The writer observed many more stations than those cited below. The species, listed by Countryman (1978) as Rare and Endangered, does not require any legal protection.

Recent Vermont records are: Addison Co., Ferrisburg 1981, Middlebury 1981, New Haven Junction 1981; Bennington Co., Bennington 1984 observation; Chittenden Co., Burlington 1968,

1980, 1981, 1985, Colchester 1981, Essex Junction 1981, Richmond 1981, South Burlington 1981; Franklin Co., Highgate 1982, St. Albans 1980, Sheldon 1982, Swanton 1982; Lamoille Co., Johnson 1981; Rutland Co., Rutland 1981; Washington Co., Montpelier Junction 1981, Moretown 1983 observation, Waterbury 1979, 1981; Windham Co., Bellows Falls 1981, Brattleboro 1978, 1981, Jamaica 1981, Vernon 1982; and Windsor Co., White River Junction 1981.

**Panicum rigidulum**

*Panicum rigidulum* Nees [= *Panicum agrostoides* Spreng.], panic grass, is a native found on damp sunny banks and shores in southeastern Vermont. Countryman (1978) listed it as Rare and Endangered, citing stations from Hartland (1892–94) and Newfane (1892). The contemporary records include some large weedy colonies, suggesting that the species is increasing in distribution and numbers of individuals, and it should be dropped from Rare or Endangered lists in Vermont.

Recent Vermont records include: Windham Co., Bellows Falls 1939, Dummerston 1982, Guilford 1982, Rockingham 1983, and Vernon 1931, 1982, 1984.

**Sporobolus asper**

*Sporobolus asper* (Michx.) Kunth, rough dropseed, was discovered in Vermont in 1877 on Thompsons Point, Lake Champlain, Charlotte, Chittenden Co., by Cyrus Pringle (Brainerd et al., 1900). Pringle's station was never re-located, and is assumed extirpated. The point is now a developed residential area. In 1983, a population of circa 50 plants was found on sunny calcareous ledges at the narrow apex of Button Bay Point, Lake Champlain, Ferrisburg, Addison Co. (*Zika 7770* VT). The habitat is seasonally scoured by lake ice.

Button Bay Point, in Button Bay State Park, receives heavy recreational use in the summer. Boaters, swimmers, and hikers tend to congregate there. *Sporobolus asper* is recommended for Endangered species status in Vermont (10 V. S. A., Chapter 123) to protect it from possible development of the site.

**Sporobolus cryptandrus**

*Sporobolus cryptandrus* (Torrey) A. Gray, is a native North American perennial from south and west of Vermont. Sand dropseed was first collected in 1980 (*Weir 40* MASS) in a Rutland railroad yard. It did not persist there, but subsequent introductions became well established on open sandy ground or railroad embankments in Colchester (Zika et al., 1983) and in the lower Connecticut and West River Valleys in Vermont.

Recent Vermont records are: Bennington Co., Pownal (limestone cliff) 1982; Washington Co., Waterbury 1981; Windham Co., Jamaica 1981, Rockingham 1983; Windsor Co., Springfield 1981, and White River Junction 1981.

*S. cryptandrus* is too common to require legal protection in Vermont. Dore and McNeill (1980) note it has spread rapidly along rails and roads in Ontario. They suggest that the pericarp, sticky when wet, aids its dispersal. Although a tall grass (up to 1.3 m), sand dropseed is inconspicuous when the inflorescence does not expand beyond the apical leaf sheath.

**Tridens flavus**

*Tridens flavus* (L.) A. S. Hitchcock [= *Triodia flava* (L.) Smyth] is a tall, dark purple and handsome perennial. Purpletop was discovered in Vermont in 1912 in Townshend, Windham Co. (Wheeler, 1913). With no subsequent documentation, Countryman (1978) placed it on the state Rare and Endangered species list. Like *Leptoloma, Tridens* recently colonized sandy roadsides at lower elevations in southeastern Vermont. Conspicuous in the autumn flora of the West and Connecticut River drainages, purpletop was as far north as Westminster on the banks of Interstate 91 in 1982. By 1984, it had advanced along the freeway 15 km north into Springfield. D. M. Ladd (1979, unpubl. M.S. thesis, S. Ill. U., Carbondale) did not report *Tridens* in Washington Co., although he collected along the major railroad lines. In 1981, the Montpelier population was located in a railroad yard. *Tridens,* now common and weedy, does not require legal protection in Vermont. It is also spreading north in New Hampshire, and was recently found in southern Canada (Catling et al., 1978).

Recent Vermont records are: Bennington Co., Dorset 1983; Washington Co., Montpelier 1981; Windham Co., Brattleboro

1981, Dummerston 1981, Guilford 1982 observation, Jamaica 1981, Putney 1981, Rockingham 1981, Townshend 1981, Westminster 1982 and 1984 observations; and Windsor Co., Springfield 1984 observation.

**Zea mays**

*Zea mays* L., maize, is commonly cultivated and repeatedly adventive in Vermont. Flynn (1911) reported corn as "occasional in waste places" in the vicinity of Burlington. Kittredge (1939) noted *Zea* was "occasional along streams and fencerows" in the Woodstock area. Seymour (1969) stated it "occurs occasionally." D. M. Ladd (1979, unpubl. M.S. thesis, S. Ill. U., Carbondale) found it wild in Washington Co., in Berlin, Middlesex and Roxbury. There were no vouchers supporting the literature reports, and corn was omitted in the most recent state checklist (Atwood et al., 1973). These collections are apparently the first for Vermont: Chittenden Co., Burlington, 1980 and 1981 (*Zika 2365* MASS, NEBC, VT; *Zika 5252* VT); Rutland Co., Rutland, railroad yards in 1980 and 1981 (*Zika 1999* MASS, VT; *Zika 5276* VT), and pasture, Shoreham, 1984 (*Zika 8430* VT).

## SUMMARY

Several trends were observed in the last 20 years. They are summarized as follows:

(1) Most of the species studied, except *Glyceria acutiflora* and *Sporobolus asper,* were under-represented in herbaria at the start of the study in 1980, as suggested by Countryman (1978). However, *Glyceria acutiflora* and *Sporobolus asper* maintained their status as rare natives in Vermont. They are recommended for state Endangered species status.

(2) Populations of *Aristida dichotoma, Eragrostis capillaris, Leptoloma cognatum, Panicum dichotomiflorum, Sporobolus cryptandrus,* and *Tridens flavus* recently advanced north in Vermont. This movement parallels the northern spread of several grasses in New York state (Smith, 1965) and into Ontario (Dore and McNeill, 1980). *Poa bulbosa* L. is another recent arrival in the northeast, in Massachusetts (Grayum and Rohman, 1986) and Vermont (Zika, 1986).

(3) Five native species formerly considered Rare and Endan-

gered in Vermont (Countryman, 1978) are increasing and aggressively colonizing disturbed ground and are no longer Rare: *Eragrostis capillaris, E. frankii, Leptoloma cognatum, Panicum dichotomiflorum,* and *Tridens flavus.* In addition, the natives *Aristida dichotoma* and *Sporobolus cryptandrus,* essentially absent 20 years ago, are now widespread and weedy.

(4) Mobile (weedy) taxa spread along transportation corridors, where open, early successional habitats are maintained and means of long-distance dispersal are readily available. Railroads are important or primary habitats for the three *Aristida* species, *Diplachne acuminata, Eragrostis capillaris,* and *Panicum dichotomiflorum.* The annual cultivar *Zea mays* repeatedly occurs as a railroad yard weed. Sunny roadsides provide habitat for *Eragrostis frankii, Leptoloma cognatum, Panicum dichotomiflorum, Sporobolus cryptandrus,* and *Tridens flavus.*

(5) Few collectors are active in Vermont in the autumn. The distribution and abundance of the *Aristida* and *Sporobolus* taxa, as well as *Tridens flavus,* may have been poorly understood owing to their tardy anthesis (late August–October).

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# THE VASCULAR FLORA OF SEASHORE STATE PARK, VIRGINIA BEACH, VIRGINIA

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GERALD F. LEVY, AND JUDITH L. KERNELL

## ABSTRACT

Floristic studies of Seashore State Park, A National Landmark and region of floristic interest for more than a century, are reviewed. The present flora consists of 558 species in 306 genera in 107 families, including several Alleghenian species which reach their southern limit in the park. Changes in habitat have resulted in the loss of numerous species.

Key Words: vascular flora, Cape Henry, southeastern floristics, southeastern Virginia

## LOCATION

The 2770 acres (1121.85 hectares) of Seashore State Park occupy the greater part of Cape Henry forming the southern entrance to Chesapeake Bay. It is located in the city of Virginia Beach (formerly Princess Anne County), Virginia, at 36° 55′N and 76°00′W. The park's northwest boundary includes approximately .75 miles (1.21 kilometers of beach fronting on Chesapeake Bay and abuts Fort Story Military Reservation (Figure 1). On the west and south are residential areas. The remaining park boundary, approximately 5 miles in length, is composed of Long Creek, Broad Bay, and Linkhorn Bay, tributaries of the Lynnhaven River.

## CLIMATE

The Cape Henry region is characterized by mild winters and long humid summers. Mean annual temperatures vary little, but average about 60°F (15.6°C) due to the modifying influence of the Atlantic Ocean and Chesapeake Bay. Daytime highs during the cold season are usually near 50°F (10°C) with nighttime lows about 30°F (−1°C). Temperatures range from over 100°F (38°C) to as

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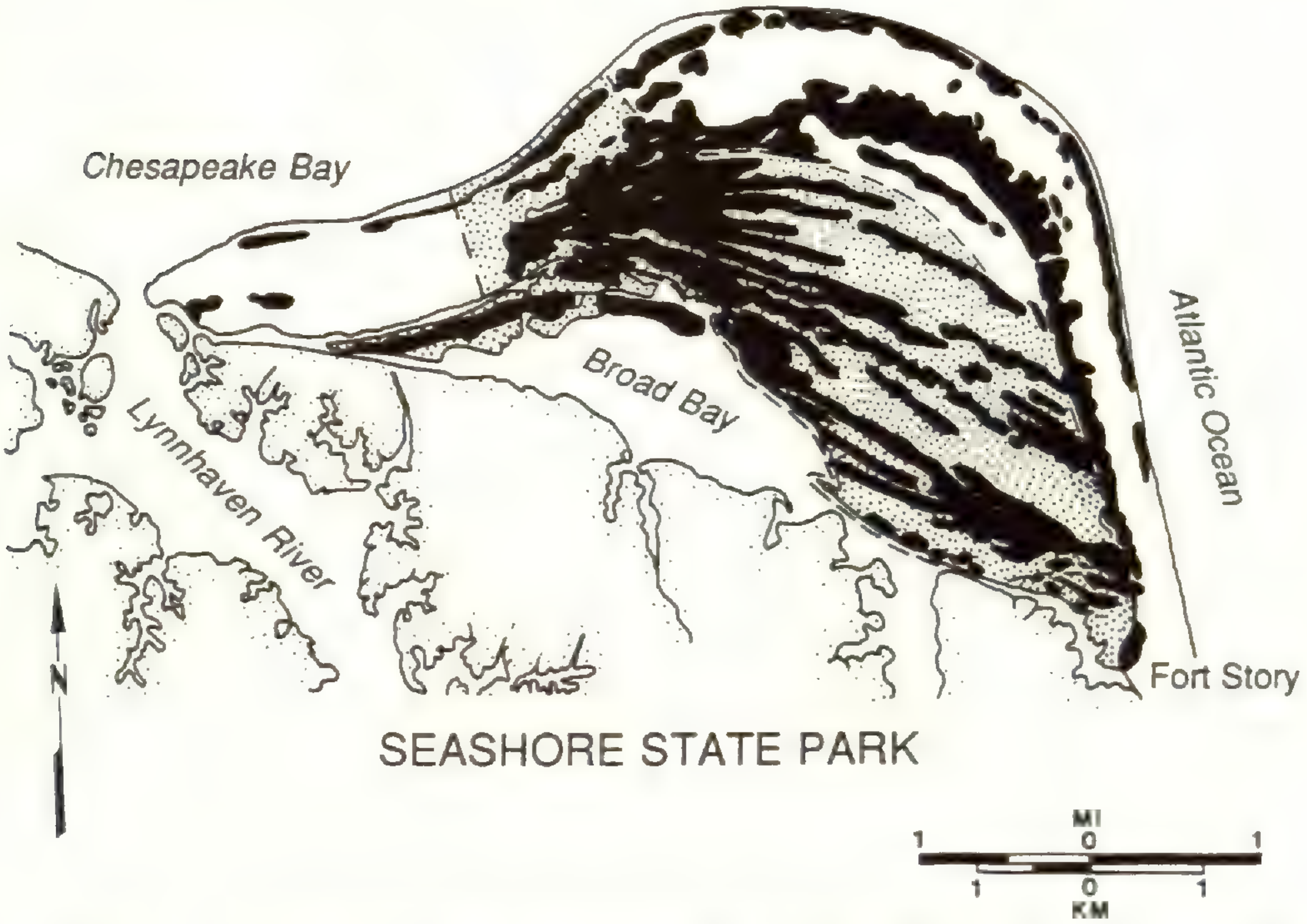


Figure 1. Map showing Cape Henry with major sand dunes (black), peaty swales (small stipples), zone of low coastal dunes (large stipples). Boundaries of the park are indicated by dashed lines.

low as 5°F (−15°C). The average growing season is 259 days. Annual precipitation averages 44.22 inches (112.3 cm) and is well distributed throughout the year with a maximum in August and minima in November and April. Summer rainfall is due mainly to showers and thunderstorms (Crockett, 1970). Significant precipitation occurs on an average of 120 days of the year. In winter, the average snowfall is 6.5 inches (16.5 cm). However, yearly snowfalls are extremely variable ranging from none up to 24 inches (57 cm). Snow seldoms remains on the ground more than two or three days. South to southwest winds predominate with those from the north secondary. During the warm season, relative humidity averages near 90%. Hurricanes and other tropical disturbances occasionally affect Cape Henry and the surrounding areas. Considerable damage from wind and tidal flooding may result due to salt spray and salt water intrusion into usually fresh water habitats. Thunderstorms accompanied by severe lightning, high wind, and hail are frequent in summer and produce the greatest amount of storm damage (U.S. Department of Commerce, 1953).

## TOPOGRAPHY AND SOILS

The topography of Seashore State Park is characterized by a series of stabilized parallel dunes which traverse the arc formed by the cape's shoreline. The dunes—up to 75 feet (22 m) high—alternate with fresh water swales which lie near sea level (Figure 2). The soils of the cape, formed of winddriven marine sediments of Holocene age, are of four main types: Newhan-Duckston-Corolla (white siliceous sand), Pamlico-Fripp-Lakehurst (gray sand), Pamlico (mucky peat), and Rhappahannock (mucky peat) (Hatch et al., 1985). The white siliceous sand has a high salt content and is found on the beach, foredunes, and in the shrub zone. Gray sand is found on the extremely large secondary dune (known locally as The Great Dune), as well as on the much lower relic dune lines behind. This sand is mainly siliceous, of a light gray color (due to a slight admixture of organic materials), seldom more than three to five centimeters in depth and underlain by the nearly pure sand and fine sediments extending to the basement rock. This sand is also found on the relic dunes behind the Great Dune. The pH ranges from neutral to very acid, and the drainage is from excessive to poor (Hatch et al., 1985). Due to the extreme geologic youth of Cape Henry (less than 5000 years in its present location according to Oyler, 1984, Master's thesis, Old Dominion Univ.), there has been little time for a true A soil horizon to form. The Great Dune descends at an angle of 45° directly into a swampy swale. These swales have formed in the old interdunal areas between the relic dunes. The soils of the swales, Pamlico mucky peat, are formed of partially decomposed organic matter over the sandy marine sediments. Such soils are deep but very poorly drained and usually have fresh, strongly acidic water. The thickness of the organic material ranges from 20 cm. to 100 cm. The organic material is extremely acid (Hatch et al., 1985). Rhappahannock mucky peat is found where erosion has caused salt water intrusions into formerly fresh swales and where new saltmarshes are forming along Broad Bay and Long Creek. These soils are also deep and very poorly drained; they are composed of marsh detritus and loamy marine sediments. This soil is strongly saline as it is flooded twice daily with brackish tidal water.

## BOTANICAL HISTORY

An overview of the history of Seashore State Park is provided by E. Johnson (pers. comm., 1986). The botanical history of Cape

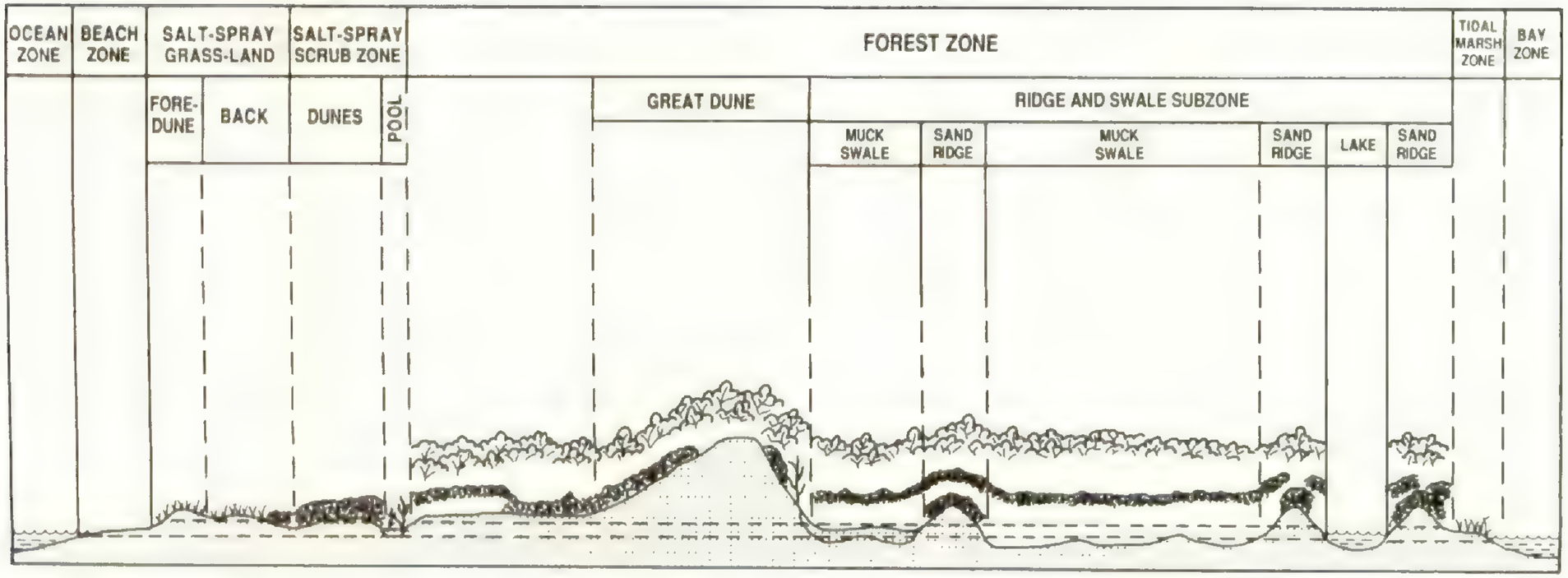


Figure 2. Diagramatic cross section through Cape Henry, showing topography and zonation of vegetation (after Egler, 1942).

Henry includes some of the earliest descriptions of North American vegetation by Europeans since the Cape is where the settlers for the Jamestown expedition first landed. But the area was visited even earlier, in 1585, by Thomas Harriot and John White, members of Raleigh's Roanoke, Carolina Expedition (Quinn, 1985) and discussed in Harriot's "A brief and true report . . ." (1590). This report was followed seventeen years later by the reports of the Jamestown settlers' first sighting of the Virginia shore on April 26, 1607 (Old Style). John Smith (1624) related: "The land white hilly sands like unto the Downes, and upon the shores great plentie of Pines and Firres. . . ." This description is valid today. The "Firres"" are *Taxodium distichum.* In 1770, the whole of Cape Henry was declared public lands at the request of prominent local landowners, an action which preserved the natural aspects of the cape for the next 100 years. However, in 1870, the Reconstruction government sold these lands to lumbering interests for one dollar per acre. Fortunately, due to the topography of the area, it could not be ditched and drained as was the Dismal Swamp, thus a large part of its forest was not destroyed. The last lumbering was done in 1927.

Drawn by reports of the unusual nature of the Great Dune, B. H. Latrobe, Capitol architect and natural philosopher, visited Cape Henry in December, 1798. He observed that the dune descends directly into the swampy "Desart" and noted that it "is overgrown with aquatic trees and shrubs; the gum, (*L. styraciflua*) the cypres (*cup. disticha*) [= *Taxodium distichum*], the maple (*acer rubrum*), the tree improperly called the sycamore (*platanus occidentalis*), the *magnolia glauca*, the wax myrtle (*myrica cerifera*) and the reed (*ar. tecta*) are the principal . . . ." He also discussed the advance of the active dune into the area behind, still called The Desart (Latrobe, 1798). There are several photographs in Kearney (1901) which document Latrobe's descriptions. Latrobe went on to say that in the preceding sixteen years the dune had grown in height and had migrated a distance of about 350 yards into the swamp killing everything in its path and speculated, "If the hills advance at an equal ratio for 20 or 30 more years, they will swallow up the whole swamp, and render the coast a desert indeed, for not a blade of grass finds nutriment upon the sand." Fortunately, this process slowed and has nearly ceased or we would not have the extensive flora found in Seashore State Park today.

There have been several studies on the flora of Cape Henry, the most complete of which is part of T. H. Kearney's "Botanical Study of the Great Dismal Swamp Region" (Kearney, 1901). Kearney's work remains a classic and is useful today. Another student of the Cape Henry flora was the intrepid Merritt Lyndon Fernald. In his first trip to Cape Henry in 1933, Fernald was surprised by the "relative abundance there of Alleghanian types, growing in close proximity to the typical coastal plain species" (Fernald and Griscom, 1935). The problems associated with botanizing in southeastern Virginia were discussed by Fernald in *Rhodora* in 1939. He wrote, "Every natural spot has to be investigated: one cannot safely pass one of them if he wishes to find all the specialities." This observation is so true of the park as many of the species are confined to single areas and are unknown in nearby habitats. The same article enumerated flora that Fernald considered native to Tidewater, Virginia. This list included over fifty species contained in our Catalog of Species (Wright, et al., 1990). On another of his trips to Virginia Beach in the summer of 1939, Fernald mentioned being taken to the station for *Osmanthus americanus* (Fernald, 1940). The only known station for this species in Virginia (Harvill et al., 1986) is within the confines of the park. Other interesting plants noted by Fernald (1935) included the orchid *Habenaria cristata,* now apparently extirpated. Fernald also noted in his Midsummer Vascular Flora of Virginia (1935) that ". . . one of Tidestrom's original collections of his *Typha angustifolia* var. *virginica* was from Cape Henry."

Because of travel restrictions during World War II, Fernald made few additional trips to this southeastern corner of Virginia, also the southeastern limit of his manual's range, but continued to publish his work based on material previously collected. His last specific publication citing flora from Cape Henry appeared in his Additions and Subtractions from the Flora of Virginia (Fernald, 1947).

A contemporary and protagonist of Fernald was Frank E. Egler (1942), who published the first work devoted exclusively to the flora of Seashore State Park. In response, later in 1942, Fernald published a diatribe against Egler in one of the longer footnotes published in Rhodora. This attack was rebutted by Egler in Rhodora in 1943. During a visit to Dr. Egler's home in the summer of 1981, he told one of us (JBW) that he never visited the park again, fearing its natural aspect would be greatly changed.

## METHOD OF INVESTIGATION

Initial field work of this investigation was conducted between September 1980 and the end of August 1982. An attempt was made to cover every section of the park at least twice during each season and to visit representative sites at least once a month. All of the marked trails were covered, as well as transects across the dune lines and, where possible, through the swales. The beach proper and foredunes, as well as the camping area which is in the shrub zone, were thoroughly covered. Attention was also given to the disturbed areas. Special efforts were made when there was radical change in the water level due to droughts or periods of excessive rainfall. One set of specimens is deposited at ODU; the other will be deposited at the park. We did not follow the advice Fernald gave Egler to examine all the relevant specimens in the Gray Herbarium (Fernald, 1942).

On one of his many collecting trips to this part of Virginia, Fernald in 1947 wrote:

> "Thus we have again demonstrated that, in spite of almost complete clearing, settling, and cultivating of many areas of Southeastern Virginia, there is plenty yet to do for the botanist who knows what to avoid as ordinary, what to collect as unusual. Almost every wholly and unmolested spot has its isolated specialties. The great problem is to locate these spots. . . . Only by learning the more conspicuous "indicators" and promptly following up their indications (before the plow or bulldozer gets there) can we find the last remnants of what originally must have been the most varied and numerically the largest indigenous flora in the Manual area. Many species found by early botanists are apparently gone but many others, not seen by them, still linger. These we want to know about before Man has destroyed them."

How much more true Fernald's statement is today, now that Virginia Beach is one of the fastest-growing cities in the nation with a population in excess of 350,000, than it was 40 years ago when Princess Anne County was a mostly agricultural county with a total population of less than 40,000 residents. In the wake of this explosive growth, it is imperative that the flora not only be documented, but that natural areas such as this park be preserved in their entireties as living museums of Virginia's botanical heritage.

## VEGETATIVE ZONES

Egler (1942) divided Seashore State Park into seven zones more or less parallel to the shoreline. These zones were generally distinct from one another due to environmental factors and the dominance of certain species. Only the boundaries of several of the zones have changed due to physical factors such as growth of a new and higher foredune and removal of the tidal gate protecting White Hill Lake. Dune building, installation of the tidal gate and construction of most of the trails were done in the 1930's. Egler's analysis is still useful, therefore, only significant changes will be discussed here.

1. Ocean Zone. Like the rest of the cape, this zone is characterized by a sandy substratum. This zone was not included either in Egler's "Checklist" or in this study, as it is unvegetated.

2. Beach Zone. This area is a gently sloping, accreting beach, generally rising no more than five feet above sea level. Like typical barrier beaches, it is divided into three parts: surf zone, intertidal zone and upper beach, the first two of which are unvegetated. The upper beach extends to the foot of the foredune. This zone is the first that has undergone considerable change since Egler's visit. In fact, the present foredune did not exist in 1940; it is the result of dune growth instituted by the federal dune building project from 1936 through 1938. This new and still-growing dune now averages in height more than 15 feet above sea level (USGS, 1979). The plant community is much the same as in Egler's time with the exception of *Carex kobomugi* Ohwi which is rapidly becoming the dominant ground cover. Its existence here was one of the chief points of Fernald's attack on Egler (Fernald, 1942). Fernald did include it, however, in *Gray's Manual of Botany* in the 1950 edition (Fernald, 1950). Until 1980, *C. kobomugi* was only found in small patches in the lee of the foredune. The coal mine strike of that year resulted in over 100 colliers being anchored for months in Lynnhaven Roads, only several hundred yards off the park's beach. Although illegal, many of these ships pumped their effluent overboard at night only to have it be washed ashore by the tides. Many northeasters that winter seem to have thrown this "fertilizer" high on the foredune giving *C. kobomugi* the nutrients it needed to spread rapidly. Now, more than 10 acres on both sides of the foredune are almost covered with it. There is practically no dune erosion in these areas, seeming to

make this species ideal for dune protection. It is, however, unpopular with many local conservationists because it tends to crowd out native, more "desirable" grasses such as *Uniola paniculata*.

3. Salt-spray Grassland Zone. This next area extends from the crest of the foredune to the beginning of the Shrub Zone as described by Egler.

4. Salt-spray Shrub Zone. This zone follows but is much reduced in width, probably due to the protection offered by height of the present foredune. This protection from the wind and salt-spray has allowed the seaward advance of trees of the maritime forest. This zone has also extended several hundred yards farther inland, nearly to the foot of the Great Dune.

5. Forest Zone. Egler's "pool" subzone of his Scrub zone has now become part of the Forest Zone. The canopy here now consists of mature though somewhat stunted *Quercus virginiana* (which are suffering heavy damage from the chestnut blight fungus, *Cryphonectria parasitica*; Stipes et al., 1978), *Q. incana, Q. laurifolia* as well as several oak hybrids; mature *Pinus taeda* predominate. Still present are *Salix nigra* and *S. carolina* as well as the freshwater community noted by Egler (1942). This small freshwater swale is an excellent example of how the large swales behind the Great Dune were originally formed. The Great Dune Sub-zone has also undergone significant changes probably due also to growth of the foredune and the advancing front of the maritime forest now protecting it from direct assault by ocean winds. For centuries the dune apparently remained bare except for a few pioneer grasses as described by Latrobe (1798), Kearney (1901) and Egler (1942). Since the 1940's, the dune, with the exception of a few minor blowouts, has gradually become heavily forested with the typical Pine-Oak-Hickory community described by Egler and Kearney (op. cit.).

The nature of White Hill Lake has also changed dramatically. The freshwater lake and marsh described by Egler no longer exist in spite of information to the contrary supplied by the park. The area originally had been one of the typical fresh water interdunal swales but with a small fresh stream, the original headwaters of Long Creek, running through it. At some point, perhaps in Colonial times, beavers apparently dammed the stream, making a large pond eventually containing many large bald cypress (*Taxodium distichum*). When the Civilian Conservation Corps was developing the park's trails in the 1930's, this dam was turned

into a causeway and an automatic tide gate was installed across the stream. In the interim, rising sea level and a blowout in the dune line were causing Long Creek to become brackish. This tide gate effectively preserved the fresh water lake described by Egler. By 1975, the condition of the gate had deteriorated to the point that park personnel removed it, allowing brackish water to invade the lake and its marsh. The ancient stately *Taxodium* are now dead snags and the younger trees at the edge of the marsh are rapidly dying due to the brackish water while the marsh itself is becoming a typical salt marsh. Another large, freshwater marsh was breached during the Spring 1963 storm and is also in a state of transition. The original nature of Long Creek was documented by one of the original Jamestown settlers in a description of the first landing and exploration ". . . wee landed and discoured a little way, but wee could find nothing worth speaking of, but faire meddowes and goodly tall Trees, with such Fresh-waters running through the woods, as I was almost rauished at the first sight thereof . . ." (Percy, 1610). The upper reaches of this now intermittent stream is the home of the only reported natural stand of Atlantic White Cedar (*Chamaecyparis thyoides*) remaining in the city of Virginia Beach (old Princess Anne County).

These fresh water marshes were undoubtedly the habitat of several species noted by earler workers including *Pontederia cordata* L., *Spiranthes* spp., *Nuphar luteum* (L.) Sibthorp & Smith, *Callitriche heterophylla* Pursh, *Juncus repens* Michx., *Rotala ramosior* (L.) Koehen, *Proserpinaca pectinata* (L.) Herbert, *Zephyranthes atamasco,* etc., which we have not found in the park and assume an extirpated.

6. Tidal Marsh Zone. Although somewhat larger, this area is the same as in Egler's time as is his Zone 7, The Bay Zone. In general, Egler's treatment of the roads and trail-sides are still adequate.

## FLORA

Seashore State Park is dominated by species belonging to the flora of the southeastern United States. Kearney (1901) considered Cape Henry to be part of the Great Dismal Swamp Region as well as the northeastern limit of the the Austroriparian area. There is little reason to disagree with his analysis today. There are, however, a number of northern species reaching or nearing

their southern limit, as well as a number of Alleghenian species (Fernald and Griscom, 1935). One set of our specimens is deposited in ODU, the other is to be kept at the park. To date, 558 species belonging to 106 families and 306 genera have been collected. These plants are listed in the Catalog of Species (Wright, et al., 1990).[2] Of these, 30 are on Virginia's Natural Heritage Program list of rare and endangered species. Only species found by the present authors are included in the Catalog. An additional 75 species listed for Cape Henry by other botanists such as Fernald, Kearney, Egler and others, are listed separately. The families are listed in the sequence found in the *Manual of the Vascular Flora of the Carolinas* (Radford et al., 1968). The genera and species are then listed alphabetically. The nomenclature is also that of Radford (except for genera or species not found therein) which follow *Gray's Manual of Botany* (Fernald, 1950), or Gleason and Cronquist (1963).

## ACKNOWLEDGMENTS

We are indebted to a dedicated group who, in one way or another, contributed to the completion of this work. Special thanks are offered to Superintendents Earnest Barker, James Guyton and Frederick Hazelwood IV who served successively during the years of this study and to their respective staffs for their cooperation and support. A major debt is owed James E. Perry III for many long hours spent identifying and verifying species. Garrie Rouse and Christopher Ludwig helped locate some rare species of special concern. Dr. Frank E. Egler gave renewed inspiration to two schoolmarms one fine summer afternoon at his Connecticut home, Aton Forest. The map of Figure 1 was generously donated by Dr. G. Richard Whittecar of the O.D.U. Dept. of Geophysical Sciences. We are also grateful to Edward Wright for helping to compile the catalog of species and for other help.

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[2] The catalog (species list) is available from the authors; a copy is also on deposit in the library of the Missouri Botanical Garden, St. Louis.

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# NEW ENGLAND NOTE

# *MYOSURUS MINIMUS* (RANUNCULACEAE) IN NEW ENGLAND WITH NOTES ON FLOWER MORPHOLOGY

BRUCE A. SORRIE

The diminutive winter annual known as mouse-tail, *Myosurus minimus* L., was discovered in Westport, Bristol Co., Massachusetts on 22 May 1988. A few hundred plants occupied bare, clayey soil of a fallow field south of Briggs Road and west of route 88 in the company of weedy species such as *Capsella bursa-pastoris* (L.) Medic., *Erophila verna* (L.) Chevall. ssp. *praecox* (Steren) Walters, *Veronica p. peregrina* L., *Plantago rugelii* Dcne., and *Chamomilla suaveolens* (Pursh) Rydb. Collections (*BAS 4179*) have been deposited at GH and in my personal herbarium.

Although this weedy species enjoys a wide range in temperate North America and Eurasia and is therefore not unexpected in New England, a search of available floras, atlases, checklists, and specimens at GH indicate that it heretofore has not occurred closer than southeastern Pennsylvania and southeastern Virginia as an adventive, and southern Ontario as a native species. Available collections amply demonstrate its preference for vernally wet, clayey, circumneutral to alkaline soil. Native populations apparently often occur on or near limestone outcrops, while adventives have been recorded most frequently from fallow fields and roadside depressions.

There appears to be some confusion in the literature about flower color, morphology, and presence of petals. Although the Westport *Myosurus* was flowering and fruiting prolifically, there was but a single flower per scape, apparently the norm for this species. Flower color was an attractive, pale lilac-pink color, not yellowish green or whitish as stated in the manuals, and was due to the presence of five narrow petals which fit precisely against each greenish sepal. Each sepal bore a slender whitish spur which pointed downward, closely appressed to the scape. Sepal and petal blades are essentially identical in size and shape, such that on dried specimens, when the latter have lost their distinctive color, one may distinguish them only by carefully teasing the two apart. Thus, unless careful examination is made, dried specimens may

appear to lack petals. Westport plants retained their lilac-pink petals even as the receptacle elongated into the diagnostic "mouse-tail," finally dropping along with the sepals as maturation of the mouse-tail neared. The stamens were topped by ovate, maroon anthers, which dropped some time before the petals.

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RHODORA, Vol. 92, No. 870, pp. 105–107, 1990

# NEW ENGLAND NOTE

## *AMPHICARPUM PURSHII* (POACEAE), A GENUS AND SPECIES NEW TO NEW ENGLAND

BRUCE A. SORRIE AND PETER W. DUNWIDDIE

The annual peanut-grass *Amphicarpum purshii* Kunth is one of two species in the genus, both inhabiting the Atlantic Coastal Plain of North America. These species occupy seasonally wet or inundated pine savannas, flatwoods, exposed pond bottoms, depressions in pine barrens, cranberry bog margins, spoil banks, and the like. *Amphicarpum purshii* ranges from southeastern Georgia to the New Jersey pine barrens where it reaches its northern limit in Ocean County.

We wish here to report a major range extension to Nantucket Island, Nantucket County, Massachusetts. On 5 October 1988, the authors botanized several areas in the eastern part of the island, including a large area south of Sesachacha Pond recently acquired by the Massachusetts Audubon Society. In two kettle-hole pondlets, locally known as the Pine Knoll Ponds, populations of *Amphicarpum purshii* were found. Both pondlets were nearly dry, due to the below-average rainfall period extending since 1985. The populations occupied very small portions of the available habitat, at the ecotone between the more densely vegetated, shallowly sloping, exposed "shore" of the pondlets and the less densely vegetated, nearly flat bottom. Associates were *Agrostis scabra* Willd., *Calamagrostis canadensis* (Michx.) Nutt., *Eleocharis obtusa* (Willd.) Schultes, *E. olivacea* Torr., *E. smallii* Britt., *Fimbristylis autumnalis* (L.) R.&S., *Rhynchospora capitellata* (Michx.) Vahl, *Xyris difformis* Chapm., *Juncus canadensis* J. Gay, *J. pelocarpus* Mey., *Lycopus amplectens* Raf., *Gratiola aurea* Muhl., *Utricularia subulata* L., and *Euthamia tenuifolia* (Pursh) Nutt. There was no sign of the state endangered *Sabatia campanulata,* originally found here in 1899 and rediscovered in 1986, but the variable ecology of these groundwater wetlands makes species inventory a long-term affair. BAS had visited these ponds on at least three occasions back to 1980 without encountering *Sabatia* or *Amphicarpum.*

The distance from Nantucket Island to Ocean County, New Jersey, is about 400 km (240 mi.) and represents one of the most

striking of the New England disjuncts. Nearly all of the Coastal Plain species which inhabit New England also have been documented from Long Island, New York, notable exceptions being *Eleocharis microcarpa* Torr., *Scirpus etuberculatus* (Steud.) Kuntze, *Sabatia kennedyana* Fern., and *Sclerolepis uniflora* (Walt.) BSP.

On Nantucket, *Amphicarpum* plants were all less than 30 cm (one foot) tall, but distinct due to the long-exsert, strict inflorescence and ascending, two-ranked, hispid leaves. On collecting specimens, we noted that most plants possessed a small bud-like growth at the end of one to a few stoloniferous branches. These, of course, are the fertile subterranean spikelets which give the plant its generic and vernacular names. Dissection of several aerial spikelets yielded a viscous substance but no mature grains, indicating that they were not viable. Recently Cheplick and Quinn (1988) have shown that aerial fertile spikelets may be produced abundantly following fires and that such aerial seeds may have a higher rate of germination than subterranean ones. With the nearly complete lack of major disturbance factors such as fire and grazing, now extending for many decades (Dunwiddie, 1989), the Nantucket *Amphicarpum* populations have no doubt been forced to reproduce solely via cleistogamy. What effect, if any, this restriction has had on the species' gene pool and its ability to adapt at the northern limit of its range is unknown.

Apart from *Trichomanes* gametophytes discovered in 1976 in Massachusetts (McAlpin & Farrar, 1978), *Amphicarpum* is the first new genus of native vascular plants to be discovered in New England since *Collinsia* (1935, Vermont), *Valerianella* (1933, Connecticut), and *Sclerolepis* (1905, New Hampshire). This information was determined from specimens at NEBC, from Mehrhoff (1983), and from discussions with Les Mehrhoff (Connecticut) and Liz Thompson (Vermont).

Specimens of *Amphicarpum purshii* (*Sorrie & Dunwiddie 4495*) have been deposited at GH, NEBC, and MASS.

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# BOOK REVIEW

Mario Di Gregorio and Jeff Wallner. 1989. *A Vanishing Heritage: Wildflowers of Cape Cod.* Pp. xiv + 169. Mountain Press Publishing Company, Missoula, Montana. ($9.95 paper)

A popular illustrated guide to Cape Cod wildflowers for the "tourist and dedicated naturalist" should be a worthy and useful contribution. At first glance this volume seems to fill the bill with its handy-sized, attractive format and well-reproduced color photographs. However, a critical examination of the book dispels one's initial enthusiasm.

According to the authors, their work "is an appreciation, a guide, and a plea for protection." The objectives are fulfilled in part, but unfortunately the facile essays contain much misinformation.

Altogether the volume includes 66 wildflowers, a selection from some 1300 species of vascular plants recorded for Cape Cod. Increased coverage might have been obtained by doubling the illustrations from one to two per page of photographs. For the most part, the subject selection is good and the user will find a reasonable sampling of the Cape's more characteristic wildflowers. However, one misses such common and typical plants as the bayberry and catbrier, starflower, sweet pepperbush, the several hollies and the omnipresent blueberries, viburnums and honeysuckles.

The wildflowers featured are grouped conveniently by their local habitats ("Woodlands," "Ponds and Bogs," "Sandplains: Heaths and Pine Barrens," "Saltmarsh," "Dunes and Beaches"). Occasionally there is a lapse in habitat placement: *Lilium superbum* is not a saltmarsh species! Each subject is treated with a page of prose plus a facing full-page color photograph. Although there are good photographs, the majority fail to match the quality found in other contemporary wildflower guides; the photographs are often poorly focused or have inadequate depth-of-field. Often they fail to include useful vegetative or habitat details which are especially necessary when other descriptive information is meager.

The text is strong on plant lore but relatively weak in information needed for identification. Common and scientific names, flowering dates and habitat are given, but essential family names

are lacking; only common names are indexed, an unfortunate omission.

In addition to the habitat chapters are two others, entitled "Alien Species" and "Living on the Edge: Rare and Threatened Wildflowers." Although these are legitimate topics, the choice of wildflower examples in each seems poor. As aliens, why select "benign immigrants" which have such a restricted range that they will not be encountered by most users of this guide? A similar complaint applies to certain of the rarities featured. Why include *Polygala paucifolia, Trillium undulatum* or *Triosteum perfoliatum* which are not even recorded from the Cape proper, although common enough elsewhere in their range? The authors' uncritical selection of rarities is based on the State list of rare plants (1985) of the Massachusetts Natural Heritage Program, which is included in part as an appendix. This list bases rarity on range or occurrence within the political boundaries of Massachusetts rather than on the natural biological ranges of the listed taxa throughout eastern North America. The uninformed reader may be unaware that many of the so-called rarities listed (such as *Orontium aquaticum*—"Threatened" and *Opuntia humifusa*—"Special Concern") are growing in Massachusetts at the northern edge of their range, and should not be considered to be either rare or threatened when their total distribution is taken into account.

Mentioned earlier were the errors of fact that plague this guide. For example, in the Introduction one learns that our present knowledge of the Cape flora is a direct result of the "Cape Cod's summer set . . . who inundated [at the turn of the century] the herbarium collections of Harvard and the New England Wildflower Society with samples. . . ." The pioneer students of the flora (M. L. Fernald, F. S. Collins, J. M. Fogg, Jr.) and other early members of the New England Botanical Club (whose herbarium is of course the main source of our knowledge of the Cape's flora) are not even mentioned!

Those readers who are botanically oriented will also wince when they find such misstatements as: the Cape's oak-pine stand is a "monoculture" (the oak is also misidentified as the red rather than the black, *Quercus velutina*); "Lilies are a very large family of flowers, all of which develop from a fleshy bulb . . ."; "few of the members of the composite family are woody shrubs"; ". . . you can find hundreds of varieties of hibiscus in the Amazon jungle"; and, referring obviously to *Catharanthus roseus* of Mad-

agascar and its anti-leukemia alkaloids, "a small . . . pink flower of the Vinca genus found in Central America. . . ." Ornithologist Roger Tory Peterson is glibly joshed for proclaiming the cardinal flower as "America's Favorite"; the authors apparently are unaware that Peterson was accurately reporting on the result of a nation-wide survey of America's favorite wildflowers made some decades ago at the New York Botanical Garden.

There is no clue as to the authors' backgrounds, but it seems apparent that they are not botanists. They erred by not seeking a review of their guide (while in manuscript) by a competent botanist. Even so, there was available to them (but not even mentioned) the authoritative *Flora of Cape Cod* by Henry K. Svenson and Robert W. Pyle, published in 1979 by the Cape Cod Museum of Natural History. A careful study of this useful volume could have provided DiGregorio and Wallner with accurate historical information of the Cape's flora and its more important students, the suggestion of a more appropriate geographic area to cover, the wildflowers most typical and appropriate to consider for each of their chapters, the nomenclature most suitable to use for a New England area, and a model bibliography which any popular guide should provide to facilitate a visitor's possible developing interest in the native wildflowers.

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*Sabatia kennedyana* Fern. (Plymouth Gentian). A globally rare, disjunct species of the coastal plain of North America, occurring in northeastern South Carolina, southeastern North Carolina, southeastern New England, and Yarmouth County, Nova Scotia. Original artwork by Tess Feltes; from *New England's Rare, Threatened and Endangered Plants*. Crow, G. E. 1982. Reproduced by permission.

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# *A DREAM OF THE WOODS* A RECENTLY DISCOVERED PIECE OF EARLY FERNALDIANA

LESLIE J. MEHRHOFF

ABSTRACT

*A Dream of the Woods* is a poem thought to be attributable to Merritt Lyndon Fernald. This poem was recently discovered in the University of Maine Archives. A bibliographic search, queries to students of Fernald, and writing samples were employed to verify the poem's authenticity. A possible scenario of why the poem might have been written and why it went undiscovered is offered.

Key Words: Fernald, Fernaldiana, poem, *A Dream of the Woods,* Maine

Our views of early botanists are generally biased by the biographers' views of their subject's later years. Rarely are we afforded tangential views of our predecessors in their earlier years; if these early vignettes exist, they usually come from notebooks, journals, or correspondence.

In 1985, while preparing a talk for the Connecticut Botanical Society on Merritt Lyndon Fernald, I visited the University of Maine's library to consult their archives. My intention was to find a picture of Fernald's father, Merritt Caldwell Fernald, who was the first president of the State College of Agriculture and Mechanic Arts (now the University of Maine) at Orono (Rollins, 1951). The special collections librarian helped locate memorabilia of the elder Fernald. At one point she asked if I wished to see specimens, as stated on the accession card, collected by Merritt Lyndon Fernald. I was brought a package of heavy paper folded into a packet and tied with a coarse, flat string similar to a shoelace. On the outside was penned in elaborately hand-written script



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*A Dream of the Woods.* Upon opening the packet, we found 22 herbarium sheets, 17 with pressed plant specimens attached. The sheets either had a combination of specimen(s) and verse at the bottom of the sheet or just verse centered on the sheet. There were no collection data on the sheets with specimens. The poem was unsigned.

In the following poem the name which appears in parentheses at the beginning of a verse is the species of plant attached to that page.

### *A Dream of the Woods*

Merritt Lyndon Fernald

1. As seated in my city study drear,
   I linger o'er my volumes, lost in dreams,
   Sweet recollection now to me appear.
   And I again am following woodland streams.

2. [*Osmunda claytoniana* L.]
   Osmundas stout lift up their tropic fronds,

3. [*Arisaema triphyllum* (L.) Schott]
   The Indian Turnip in the peat abounds,

4. [*Tiarella cordifolia* L.]
   The Bishop's Cap holds out its fairy wands,
   While trees above are filled with heavenly sounds.

5. White-throated Sparrow, Northern Nightingale,
   With marked precision chants his matin hymn.
   The Hermit Thrush, half hidden in yon vale
   His wondrous flute now pipes from limb to limb;
   His song expanding with the dawning day.
   In silvery ripples from his breast doth flow,
   And as we pause to listen by the way,
   Our sluggish hearts with wakening hopes do glow.

6. [*Trillium undulatum* Willd., *Trillium erectum* L., *Trillium cernuum* L.]
   Wake-robins, white, and pink-and-white, and red,
   'Neath pine-trees stand, in saplings tender shade;
   The painted smiles, the red throws back his head,

The white, more shy, 'neath leaves her cheek has laid;
And as we softly o'er the morass tread,
We move with care, knowing she is afraid.

7. [*Rhododendron canadense* (L.) Torr.]
The gay Rhodora 'long the margin stands,
Forerunner of the Summer's fairer Rose;
Yet coming as does to ope Spring's bands,
She brightens every wood wherein she blows.

8. [*Caltha palustris* L.]
Marsh-marigold expands her golden globe,
By fairer flowers not at all made shy;
Her brighter hue with splendor doth enrobe
These shadowy spots, by trees shut from the sky.

9. [*Polystichum acrostichoides* (Michx.) Schott]
The Christmas-Fern new fronds has now unrolled,
Far tenderer then the leaves of last year's
These soon will cheer the forest elsewhere cold,
When neighbors die too weak to stand the strain:

10. [*Dryopteris intermedia* (Willd.) Gray]
But one besides her stands by every wrought
To thrive. The Wood Ferns o'er the ripples fling
Fair fronds, by many of fairer maiden sought;
Resisting cold for months, they fade ere Spring.

11. The Winter Wren, coy minstrel dressed in brown,
From Hemlock twig now flits to that of Spruce,
From Spruce to Fir, where now he settles down;
His effervescing song most wild and loose,
His rhythmic cadence, and his sweet sad notes,
His fluent strain, that rich metallic sound,
While sylvan plaintiveness through each strain floats,
Within our hearts responsive throbs have found.

12. [*Equisetum sylvaticum* L.,
*Equisetum arvense* L., (2 specimens)]
The Horsetail, striate stemmed, with curious joints,
Has, quick as Cadmus' army pierced the ground;
Each fairy branch in new direction points,
As guiding men to secrets yet unfound.

13. [*Trientalis borealis* Raf.]
The Trientalis, Chickweed Wintergreen,
From yonder mossy knoll reflects the sky.

14. [*Polygala paucifolia* Willd.]
Gay Fringed Polygalas those stars have seen,
So stretching out their wings attempt to fly.

15. The Flicker on yon Aspen old and dry
Now boisterous laughs and chuckles full of life,
Now whets his beak on knotty branch close by,
And pausing waits the coming of his wife;
He wisely tries the surface half decayed
And finding spot of firmer texture there,
Upon it now his whetted beak is laid;
Resounding drum-beats fill the enchanted air;
Again he laughs and once more beats his drum
Then utters still another louder shout,
Still wondering that his spouse is not yet come;
At last it seems his patience can't hold out,
With sudden dive he plunges into flight
Exposing golden pinions decked with red.
We stand enraptured by this gorgeous sight
Scarce conscious that our Sorcerer has fled.

16. [*Eriophorum spissum* Fern.]
The Hare's-tail spreads the bog with ermine fleece,

17. [*Coptis groenlandica* (Oeder) Fern.]
The Gold-thread's metal fibres pierce the loam,
Her glossy leaves above robe every crease,

18. [*Viburnum cassinoides* L.]
While Withe-rod heaps the margin high with foam.

19. [*Andromeda glaucophylla* Link, *Chamaedaphne calyculata* (L.) Moench, *Ledum groenlandicum* Oeder]
Andromeda, Cassandra, and Wild Tea
Aristrocratic circles here have made;

20. [*Kalmia polifolia* Wang.]
Pale Laurel, scarce so noble as these three,
With tottering step has lingered in their shade.

21. [*Arethusa bulbosa* L. (6 specimens)]
Shy Arethusa becks me cross the stream,
And as I near approach my Grecian maid,
A book dropped to the floor disturbs my dream,
And thoughts of Nymphs and Naiads quickly fade.

22. As when one wanders thoughtful through the wood,
New inspirations come from every sod,*
So after this 'tis easier to be good;
My heart o'erflows, for I have been with God.

## DISCUSSION

The obvious question is whether or not this poem was actually written by Merritt Lyndon Fernald. I suspect the following scenario.

Young Fernald came from Orono to Cambridge in 1891 at the age of 18 (Merrill, 1954). There is no evidence in his early correspondence with Sereno Watson (now at the Gray Herbarium Library Archives) that he had ever lived away from home before enrolling in the Lawrence Scientific School of Harvard University. The same correspondence shows that he was very fond of the out-of-doors and that he had already spent many hours afield botanizing. It is easy to imagine Fernald being homesick for both his family and his beloved Maine woods and bogs.

I suspect that he wrote this poem and either brought it to his family home while on holiday or mailed it to his family. His father kept the packet of specimens with his personal things and when these came to the University Archives, this "collection" came along with them.

In an attempt to ascertain whether or not Fernald wrote this poem, I first checked the bibliography of Fernald's writings prepared by Elmer Drew Merrill and published in the *Biographical Memoirs of the National Academy of Science* (Merrill, 1954). This collection is a compendium of Fernald's published writings. If, as I suspect, this poem has gone unnoticed, it is not surprising that *A Dream of the Woods* does not appear in this bibliography.

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* The only word that is unclear in the entire poem occurs on page 22, line 2. The first letter cannot be distinguished. The word is either rod or sod. Unfortunately, either word could fit the tenor of the poem and neither gives clearer meaning to the verse.

I next spoke with some of Fernald's former students who might have heard him speak about his early experiences. Most notable amongst these was Dr. Bernice Schubert of Harvard University who was close to Professor Fernald in his later years. None of those queried knew of anything like *A Dream of the Woods.*

Finally, I checked the handwriting of the poem against herbarium specimens that had handwritten labels prepared by Fernald. I chose specimens from the New England Botanical Club Herbarium (*Carex oronensis, Carex chordorrhiza,* and *Pedicularis furbishiae*) that had been collected by Fernald around the same time as I suspected that the poem might have been written. Letters, both upper and lower case, from the labels written by Fernald clearly matched those of the poem.

Botanists frequently hold the image of Fernald as a stolid fieldworker, a sharply tongued critic, and a man obsessed with advancing our knowledge of the northeastern North American flora with little time for anything else. The mention of birds in the writings of Fernald seems out of place. In the last verse, the line ". . . for I have been with God" seems paradoxical to our image of the calculating scientist, as many people view Fernald. I suspect that this is supposition on the part of those that view him in this light.

First we must remember that Fernald's biographers have not delved deeply into his personal life. Second, Fernald was not an evolutionary biologist in current sense, so the mention of God, especially in his early writings, is not incongruous. Lastly, there are occasional glimpses in the literature of a Fernald who shows great interest in the more personal aspects of his student's lives, especially their children [cf. Raup letter, 1985, Hodge and Howard comments, (Proceedings NEBC 800th Meeting, 1986)]. Dr. Eugene Ogden once told me that to get Fernald to change the subject from an unpleasant topic, he only had to ask Fernald how his children were.

The key to a side of Fernald that doesn't usually come out, a sentimental side, comes from an anecdote related by Arthur Stanley Pease in his biographic sketch of Fernald (Pease, 1951). Pease recounts how when, "as a thoughtless youth, he remarked that a certain investigation, even if carefully pursued, could only have sentimental value." Fernald responded by saying, with a good deal of feeling, "This world would be a pretty poor place if there were no sentiment in it" (Pease, 1951).

I suggest that this poem seems to be an expression of sentiment by a youth who loved the wilds of his native state and who, by taking a job in the city, missed them very much. This same sentimental youth grew to be one of the most knowledgeable students of the vascular flora of eastern North America, a highly respected phytogeographer, and a gifted teacher. All this accomplishment was in no small part due to his appreciation for nature and his first-hand acquaintance with plants as the basis for detailed botanical knowledge. *A Dream of the Woods* should be added to the list of Fernaldiana as an example of Fernald's strong bond to nature.

## ACKNOWLEDGMENTS

I thank the staff of the Special Collections Department, Raymond H. Fogler Library, University of Maine, Orono, for bringing these "collections" to my attention. Sally Rooney, of the Botany Department at the University of Maine, helped immensely by checking my typed transcription against the original poem. Lynn Aspland, Carol Paluch, and Diane Tyler have typed drafts of this manuscript. I checked with Drs. W. Drury, E. Ogden, G. Rossbach, B. Schubert, and R. Tryon to see if they had heard Fernald mention this work. To them, I am especially grateful for their time and for the reminiscences of their professor they shared with me. T. Mehrhoff, T. Philbrick, S. Rooney, and B. Schubert made helpful comments on earlier drafts of this manuscript.

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# THE FIRST RECORDS OF *GNAPHALIUM SYLVATICUM* (ASTERACEAE) AND *EMPETRUM EAMESII* SSP. *ATROPURPUREUM* (EMPETRACEAE) IN NEW YORK STATE

PETER F. ZIKA

## ABSTRACT

Two additions to the native state flora were encountered in the Adirondack Mountains of northeastern New York: *Gnaphalium sylvaticum* and *Empetrum eamesii* spp. *atropurpureum.* Both taxa are recommended for state endangered species status.

Key Words: Endangered species, *Empetrum eamesii* ssp. *atropurpureum, Gnaphalium sylvaticum,* Biosphere Reserve, Adirondacks, New York State

Two native species, previously unrecorded in the New York State flora, were discovered during field work in 1989. Populations of both taxa are within the "blue-line" boundary of Adirondack Park and within the recently established Champlain-Adirondack Biosphere Reserve.

*Gnaphalium sylvaticum* L., woodland cudweed, is an early successional perennial with a circumboreal distribution. It has been collected in the adjacent states of Pennsylvania, where it is considered adventive (Wherry et al., 1979), and in Vermont (Seymour, 1982), where it is considered a rare native (Thompson, 1989) and was recently proposed for state endangered status (Thompson, pers. comm.). Scoggan (1978–1979) reported Canadian collections from Ontario and Quebec. The New York station was discovered in August 1989, at an elevation of 2000 feet (610 meters) along the Middle Branch of the Black River in the town of Ohio, Herkimer Co. (*Zkia and Jenkins 10723* NY, NYS, VT). About 200 *Gnaphalium sylvaticum* plants were seen, occupying north-facing openings, where an old, grassy logging road crossed the river. Most of the population was south of the waterway.

Vegetation at the site was dominated by a thick turf of *Danthonia compressa* Aust., but seedlings of *Acer rubrum* L., *Betula alleghanensis* Britt., and *Picea glauca* (Moench) Voss were observed, as well as *Agrostis scabra* Willd., *Aster acuminatus* Michx., *Dennstaedtia punctilobula* (Michx.) Moore, *Panicum clandesti-*

*num* L., *Rubus hispidus* L., *R. idaeus* L., *Uvularia sessilifolia* L., *Veronica officinalis* L., and *Viola* sp. The soil is acidic pebbly sand, overlying metasedimentary bedrock (Isachsen and Fisher, 1970).

Should the New York population be treated as native or an introduction? Two statements can be made for non-native status. First, Pease (1964), Roland and Smith (1969), and Wherry et al. (1979) do not treat it as native, but offer no explanation. Second, *Gnaphalium sylvaticum* is extremely rare in an abundant open habitat, which suggests, but does not prove, that it arrived recently rather than persisting since pre-settlement times. This argument fails to recognize that a number of native species are changing their ranges this century (e.g., many grasses in Vermont; Zika, 1990). Dispersal or recruitment difficulties could also explain the rarity of *Gnaphalium sylvaticum* in the Adirondacks, at the southern limit of its range.

Stronger arguments can be given to support native status. First, it is treated as a native in boreal habitats in our area, since it has a circumboreal distribution, by Fernald (1950), Gleason and Cronquist (1963), Scoggan (1950, 1978–79), and Seymour (1982). Second, the dominant associates and most of the minor associates at the site are native early successional species, not Eurasian introductions. Third, it is a perennial, not an annual.

Some early successional species are worthy of conservation efforts. Natives which are quite rare or local in our area and occur on naturally-eroding sites are often protected by conservation laws (e.g., *Gnaphalium supinum* L., *Arnica lanecolata* Nutt., *Lycopodium sitchense* (Rupr.) Fern., *Primula mistassinica* Michx., *Braya humilis* (C. A. Mey.) Robins., *Trisetum melicoides* (Michx.) Vasey, *Saxifraga oppositifolia* L.). *Gnaphalium sylvaticum* fits the early successional but rare or local category in New York.

Accepting *Gnaphalium sylvaticum* as a native, it can be argued it is in need of conservation in New York. The pre-settlement habitat of *Gnaphalium sylvaticum* and its associates would have been dry soil in open woods, rocky slopes, slides, cliffs, riverbanks, etc. (Fernald, 1950; Scoggan, 1950). These habitats are common in the Adirondacks (as are grassy north-facing logging roads). *Gnaphalium sylvaticum*'s presence on a logging road suggests there is (or was) another population in the area. Jerry C. Jenkins (pers. comm.) conducted extensive field work in New York's Hamilton and Herkimer Counties in 1989, and although familiar with the

station in the town of Ohio, could not locate additional stations. Ironically, the logging operation that opened the habitat for the known population could later have destroyed a nearby population in a naturally-eroding location.

New York's solitary known population of *Gnaphalium sylvaticum* is restricted to a disturbed site, where logging or recreational vehicles could extirpate the species. The persistence of woodland cudweed in New York is at present jeopardized by forest succession as well as by human activities. These data suggest *Gnaphalium sylvaticum* should be placed on the state endangered species list, under the provisions of New York law (E. C. L. 9–1503).

*Empetrum eamesii* Fern. & Wieg. ssp. *atropurpureum* (Fern. & Wieg.) D. Löve is also newly reported for the flora of New York State. Taxonomic treatments of the genus *Empetrum* vary, as Hultén (1971) points out. There is considerable variation in indument and sexual systems in some parts of North America. New York State *Empetrum* populations are divisible into two taxa. Following the nomenclature in Kartesz and Kartesz (1980) and Mitchell (1986), they are *Empetrum nigrum* L. ssp. *hermaphroditicum* (Lange) Bocher, black crowberry, and *E. eamesii* ssp. *atropurpureum,* purple crowberry [= *E. rubrum, E. atropurpureum*]. In New York the two species are easily separated by their indument and fruit color: mature purple crowberry has purple berries, white tomentum on the shoots and leaf margins, and is eglandular; black crowberry has black berries (unripe fruits can be purple), sparsely glandular shoots and leaf margins, and is not tomentose. Indument characters are most easily observed early in the growing season, on fresh shoots, but are visible in the field at least as late as September, and show clearly in dried herbarium material on older twigs under magnification.

*Empetrum eamesii* ssp. *atropurpureum* was credited to New York in *The Flora of Nova Scotia* (Roland and Smith, 1969), but New York was not included in the range descriptions of the regional manuals (Fernald, 1950; Gleason and Cronquist, 1963). Local treatments also omitted the taxon (Torrey, 1842; Peck, 1899; House, 1924; Mitchell, 1986). Purple crowberry was first collected in the high peaks of the Adirondack Mountains in 1939, but the specimen was misidentified as black crowberry. Two additional stations of *Empetrum eamesii* were located by this author in 1989. These New York records are all from Essex County:

Town of Keene, July 1989, one clone, south-facing alpine slope on Haystack Mt., elev. ca. 4700 feet (1430 meters), (*Regan & Zika 10702* NYS).

Town of Newcomb, July 1939, open exposure, in a dense *Abies balsamea* krummholz, on Santanoni Peak, elev. ca. 4600 feet (1400 meters), (*Heady 544* NYS).

Town of North Elba, July 1989, one clone, west-facing alpine slope on Wright Peak, elev. ca. 4300 feet (1310 meters), (*Zika 10684* NYS).

Both species of *Empetrum* are found in alpine zones in the northeastern United States, often within a few feet of each other. Harris et al. (1964) and others have pointed out that in New England purple crowberry tends to be found on lesser rocky peaks and the lowest alpine ridges, and drops out of the alpine community at higher elevations, where black crowberry thrives among the low heaths. Purple crowberry in New York occurs at the upper end of the transition zone between krummholz and dwarf alpine heaths, partially sheltered by dwarfed trees less than 1 meter tall. The following species have been recorded as associates: *Abie balsamea* (L.) Mill., *Betula cordifolia* Ryel., *Chamaedaphne calyculata* (L.) Moench, *Clintonia borealis* (Ait.) Raf., *Deschampsia flexuosa* (L.) Trin., *Diapensia lapponica* L., *Gaultheria hispidula* (L.) Muhl. ex Bigel., *Ledum groenlandicum* Oeder, *Maianthemum canadense* Desf., *Oxalis acetosella* L., *Picea mariana* (Moll.) BSP., *Potentilla tridentata* Soland. ex Ait., *Scirpus cespitosus* L., *Sphagnum* sp., *Spiraea septentrionalis* (Fern.) Löve & Löve, *Trientalis borealis* Raf., *Vaccinium boreale* Hall & Aald., *V. uliginosum* L. ssp. *pubescens* (Wormsk ex Hornem.) Young. In addition, *Empetrum nigrum* ssp. *hermaphroditicum* occurs on the three New York peaks with *Empetrum eamesii* ssp. *atropurpureum.* The bedrock on each of the mountaintops is acidic anorthosite (Isachsen and Fisher, 1970).

An attempt in 1989 failed to re-locate Heady's 1939 *Empetrum eamesii* ssp. *atropurpureum* station on Santanoni Peak. Thus in New York the species is represented by only two small extant plants, both along popular hiking trails. Heavy trail use in the New York alpine region is causing considerable erosion of alpine vegetation mats and soils (Ketchledge et al., 1985). Numerous unauthorized trails dissect the alpine turf, and increase the rate and zone of erosion. Trampling or erosion could destroy the pur-

ple crowberry colonies in the immediate future. These data strongly suggest that *Empetrum eamesii* ssp. *atropurpureum* should be placed on the state endangered species list.

Both woodland cudweed and purple crowberry are widespread in eastern Canada and northern New England; neither species is federally threatened or endangered.

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# DOCUMENTATION ON LONGEVITY OF *GOODYERA PUBESCENS* LEAVES AND UPDATE ON *TRIPHORA TRIANTHOPHORA* IN NEW HAMPSHIRE

PHILIP E. KEENAN

**ABSTRACT**

Observations on the longevity of *Goodyera pubescens* evergreen leaves are reported, as are continuing observations of the ecology of *Triphora trianthophora.*

Key Words: *Goodyera pubescens, Triphora trianthophora,* ecology, New Hampshire

To my knowledge, no one has ever bothered to find out how long the leaves of *Goodyera pubescens* (Willd) R. Br. remain evergreen in the wild. After years of good intentions, I finally marked two leaves in the summer of 1985, making sure I was tagging the newly emerged leaf of that season. The colony on which I chose to do this experiment was one of the largest and healthiest I have ever found, consisting of approximately one hundred plants, all in prime condition. In this particular station the creeping rhizomes are partially exposed on the surface of the ground, making it easy to distinguish the separate rosettes and growing tips. One clump grows entirely exposed on the surface of a rock outcropping. After the tiny emerging leaf had made sufficient growth early that summer, I tied a strip of plastic made from a plastic "baggie" to the base of the leaf. Each year thereafter I checked the two specimens. In the three succeeding years of 1986, 1987, and 1988, each tagged leaf was in excellent condition. In 1989 I checked each leaf in May, finding them still green and in good condition but less than the perfect condition of the previous years. On July 7, each leaf had succumbed; that is, it was browned and decomposing. From mid-1985 to mid-1989 is four years; I therefore conclude that the life of a leaf of *Goodyera pubescens* in this colony was exactly four years. Currently, I am tagging *Goodyera tesselata* in a like manner.

My continuing observations on *Triphora trianthophora* (Sw.) Rydb., first reported on in 1986 (Keenan, 1986), have produced some further interesting facts. The original station under observation is the classic Algonquin site of Morris and Eames (1929), found in the nineteen-twenties. I have had this station under observation since 1974, and have missed checking the site only

three or four years during the period. It has not changed at all in those sixteen years, and from their description most probably hasn't changed since Morris and Eames's day. The second station I discovered myself, in 1985, about one mile from the original site, making 1989 the fifth straight year of observation there.

The two successive years of 1986 and 1987 were extraordinary years in terms of population numbers at both of these Holderness, N.H., sites, with 1987 a bit better than 1986. For example, there were well over 5000 plants in an area measuring 100 feet wide by 1250 feet long in 1987; in 1986, the clumps ranged in size from approximately a half dozen to well over 300 plants. This extraordinary production of blooming plants resulted in some exceptional specimens. One plant had a double flower! Another plant, the most vigorous I've ever seen, had a very thick stem branching into two smaller ones, each of which had four buds, for a total of eight buds on a single plant. The usual maximum complement is six buds. I have photographic documentation of this monstrosity. In 1987, I found my first "albinos" of *Triphora*: cream-white leaves and ovary/fruit, with pale lavender stems.

Several plants were 12″ (30 cm) in height from above-leaf surface, taller than usual. Most of the plants were in the 4″–8″ (10–20 cm) height range; even the smallest plants at 2″ (5 cm) had one or two buds. In one representative population sample of approximately 110 plants growing typically bunched together, the breakdown in bud totals was as follows: 30 plants with one bud, 75 plants with two buds, and 5 plants with three buds. Four-bud plants occur occasionally, while those with five and six buds are exceptional.

In 1988, the population explosion of the two previous years ceased abruptly, with more "normal" numbers prevailing. The smaller numbers continued in 1989, the plants numbering in hundreds instead of in thousands.

In 1989, there were several consecutive "colder" nights. August 7, 8, and 9, were all "colder than normal." On the 7th, following four straight days of high heat and humidity, a cold front went through early in the evening, dropping the temperature into the forties. *Triphora* bloomed on the 9th (a major flowering), 11th (just a few), and 12th (a big day but not as big as the 9th). On the 10th, most of the flowers that had opened on the 9th retained more color and freshness than is usual the day after, perhaps because of the colder temperatures. Normally, the flower on the

day after is clearly "wilted" in appearance. Ninety-nine percent of blooming plants on August 12 had but a single flower open. On this day, *Triphora* was blooming in the rain. Interestingly, on many plants, the light showers knocked off a lateral sepal, either the right one or the left, and sometimes the dorsal sepal as well. I also have photographs of this condition.

Though the literature stresses the habitat for *Triphora* to be deep pockets of accumulated beech leaves (Brackley, 1985; Case, 1987; Luer, 1975), my experience has shown some plants actually growing close to the road (within inches of the hottop) in superficial mineral soil, such as fine gravel deposited there by winter road sanding and/or bituminous resurfacing in the summer. Close examination, however, shows decomposing leaves beneath the thin veneer of gravel. Apparently it does not grow in predominantly mineral soil.

The favored growing site for these plants is alongside fallen decomposing tree trunks and logs of beech, but never on top of these logs, except when the log has decomposed almost completely into soft "soil" humus. The beech leaf depressions are second in preference, at least at these two stations. *Triphora* apparently does not do well with competition; wherever there is much herbaceous or sapling growth on the beech forest floor, this orchid tends to significantly decrease in numbers or be entirely absent. Only *Epifagus virginiana* (L.) Bart. is a common herbaceous companion plant here, with a few hemlock seedlings in very scattered clumps.

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# *ASTER ANTICOSTENSIS,* AN ENDEMIC OF NORTHEASTERN NORTH AMERICA: BIOLOGY AND CONSERVATION

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## ABSTRACT

*Aster anticostensis* is endemic to the Baie des Chaleurs (Gaspé), Anticosti Island, and the Saint John and Aroostook River basins (Quebec–New Brunswick–Maine). It was long confused with *A. novi-belgii.* It is found in the geolittoral zone along fast-flowing rivers. Eight sites are known, five of which were rediscovered in 1988. The species is rare throughout its range, but it has a more precarious status (endangered) in New Brunswick and Maine, where the taxon is reported here for the first time. Disturbances of the river banks as a result of human activity and regulation of water flow due to dam construction are the main factors threatening survival of this plant.

Key Words: *Aster anticostensis, Compositae,* endemic, conservation, Quebec, New Brunswick, Maine

## INTRODUCTION

*Aster anticostensis* Fernald is a species endemic to northeastern North America; it has long been confused with *A. novi-belgii* L. With the latter it belongs in section *Dumosi,* subsection *Foliacei,* characterized by a basic chromosome number of x = 8 and foliaceous phyllaries (Semple and Brouillet, 1980). The epithet *anticostensis* was applied only to the type collection. According to Fernald (1950), the other Asters reported under this name (e.g., Marie-Victorin and Rolland-Germain, 1969) do not correspond to the type description. Re-location of the taxon and determination of its chromosome number, under the name *A. gaspensis* Marie-Victorin, have been reported by Brouillet and Labrecque (1987). The nomenclatural history was discussed in detail in that paper and is summarized here in Table 1.

According to Brouillet and Labrecque (1987), *Aster anticostensis* is an allopolyploid derivative of *A. borealis* (T. & G.) Prov. and *A. novi-belgii.* Following this hypothesis, *A. anticostensis* would have an eastern origin and thus would not represent a disjunct, cordilleran taxon as suggested by Fernald (1915) and Marie-Victorin (1932).

Table 1. Taxonomic treatment of *Aster anticostensis* Fernald.

| | |
|---|---|
| Fernald, 1915 | *A. anticostensis* Fernald |
| Marie-Victorin, 1932 | *A. gaspensis* Marie-Victorin |
| Fernald, 1950 | *A. johannensis* p.p. |
| | *A. anticostensis* Fernald |
| Cronquist, 1952 | *A. gaspensis* Marie-Victorin |
| Cronquist, 1958 | *A. johannensis* Fernald |
| Boivin, 1966 | *A. novi-belgii* L. var. *villicaulis* (Gray) Boivin |
| Boivin, 1972 | *A. hesperius* Gray var. *gaspensis* (Vict.) Boivin |
| Scoggan, 1979 | *A. novi-belgii* L. var. *novi-belgii* |

## METHODS

Previously known populations of *Aster anticostensis* were researched in August of 1988; the main biotic and abiotic characteristics of the habitats of these populations were noted (Table 2), as well as the status, area and density of the populations. The types of *A. anticostensis* (GH) and *A. gaspensis* (MT) were compared to determine correct nomenclature of the plants examined in the field. Specimens of this and related taxa were examined in CAN, DAO, GH, ISC, MO, MT, NEBC, NY, TRT, UNB, WAT and WIS.

## DISTRIBUTION

*Aster anticostensis* has been found only on Anticosti Island, in the Baie des Chaleurs (Gaspé) and in the Saint John and Aroostook River basins (Figure 1). This is the first report of this species for New Brunswick and for the U.S.A. (Maine). Although the taxon was collected earlier, it was incorrectly identified. Some specimens in the Gray Herbarium from Lake Mistassini and the James Bay region were identified as *A. gaspensis* by Cronquist (1947). Upon examination, it was found that these individuals belong to *A.* "*longifolius*" (*sensu* Semple and Heard, 1987) and not to *A. anticostensis*.

## HABITAT

Except for the type locality on Anticosti Island, the range of distribution of *Aster anticostensis* lies within the 2250–2500 degree-day zone; i.e., the Baie des Chaleurs and Saint John River valley (Rousseau, 1974). The northern limits of several taxa, such

Table 2. Main habitat parameters and status of populations of *Aster anticostensis* as observed in 1988.

| Population | Slope | Substrate | % Surface Rock | Drainage | Population Size | Number of Individuals |
|---|---|---|---|---|---|---|
| Somerville (N.B.) | 3–5% | gravel | 98 | good | 3 individuals over a distance of 100 m. | 3 |
| Matapédia | 5% | calcareous gravel | 95 | good | approx. 1 km × 10 m | several thousand density about 1 ind/m² |
| Bonaventure | 2–3% | calcareous gravel | 95 | good | 1 km × 10 m (300 m east side of the bridge, 700 m west side) | several thousand density about 0.5 ind/m² |
| Grande-Rivière | 3% | gravel on slate | 90 | very good | approx. 1 km × 10 m | several thousand density about 1 ind/m² |
| Grande Rivière 2 | 1% concave | calcareous gravel | 95–50 | good | approx. 2 km × 10 m | several thousand density about 1 ind/m² |
| Petit-Pabos | 2–3% eroded | calcareous gravel on sand | 10 | good | approx. 1 km × 10 m | several thousand density about 1 ind/m² |

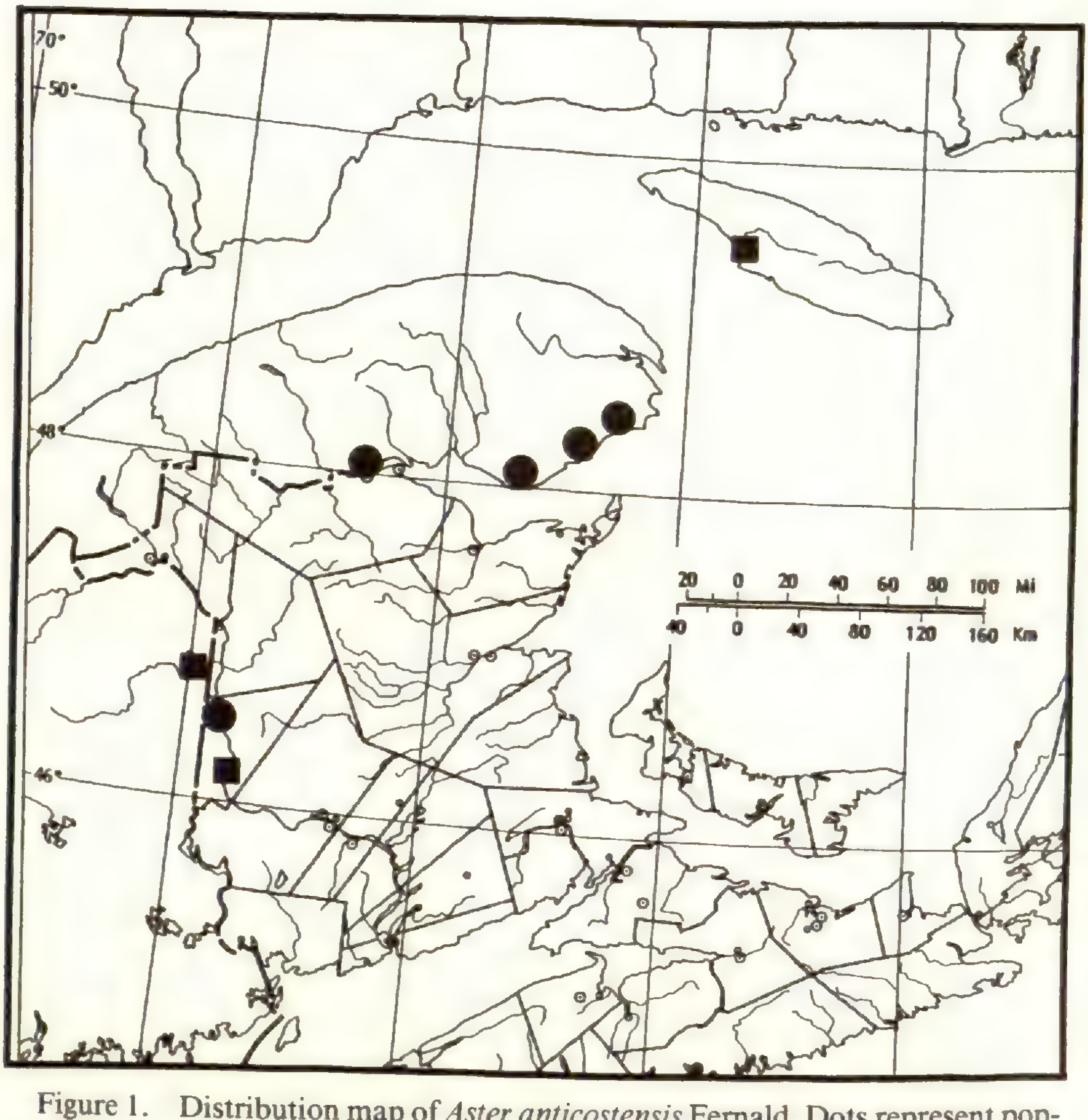


Figure 1. Distribution map of *Aster anticostensis* Fernald. Dots represent populations re-located in 1988; squares represent historical records.

as *Rhus radicans* L., *Aster cordifolius* L. and *Asarum canadense* L., are found in this area (Raymond, 1950). Although *A. anticostensis* occurs in a relatively temperate zone compared to the entire Gaspé Peninsula, the plant grows only on river strands, an environment with subarctic elements contrasting with the surrounding forest. Other plants that may be found there include: *Allium schoenoprasum* L., *Anemone multifida* Poiret, *Oxytropis campestris* (L.) DC. var. *johannensis* Fernald and *Tanacetum bipinnatum* (L.) Shultz-Bip ssp. *huronense* (Nutt.) Breitung. *Aster anticostensis* grows along rapid-flowing rivers, on the geolittoral zone (Figures 2 and 3). There is rarely more than a 3% slope. The soil is usually calcareous and coarsely sandy or gravelly in texture. *Aster anticostensis* was not found in areas where the substrate was

Figure 2. Habitat of *Aster anticostensis* along the St. John River in Somerville, New Brunswick; one clone is indicated by the arrow.

Figure 3. Habitat of *Aster anticostensis* along the Ristigouche River, in Matapédia-ouest, Québec; arrows indicate lower and upper limits of the large population on the geolittoral strand.

different (acidic or sandy) as was the case on two Gaspé rivers investigated, the Port-Daniel and Grand-Pabos. Table 2 summarizes the data collected in the summer of 1988 for the populations that were re-located.

It appears that erosion caused by ice and high water in the spring maintains populations. Gawler and Waller (1987) reached a similar conclusion for *Pedicularis furbishiae* S. Watson, a species found in the same area. Disturbance of loose soil, such as sand (as on the Grand-Pabos River) apparently prevents establishment of *A. anticostensis*. Substrate mobility can result in the burial of rhizomes or plantlets, or that type of soil may favor better-adapted species. The taxon is also absent from river estuaries, indicating that unlike *A. novi-belgii* it may be intolerant of a saline environment.

*Aster anticostensis* usually grows with species typically found along river banks or in humid environments, such as *Eupatorium maculatum* L., *Agrostis stolonifera* L. and *Apocynum cannabinum* L. It is often associated with plants that are specific to this type of habitat in the region, such as *Agropyron trachycaulum* (Link) Malte, *Dryas drummondii* Richards, *Hedysarum alpinum* L., *Muhlenbergia glomerata* (Willd.) Trinius, *Oxytropis campestris* var. *johannensis* and *Prunus pumila* L. var. *depressa* (Pursh) Bean.

## POPULATION ECOLOGY

Four of the five extant populations contain several thousand individuals. The Somerville population is reduced to three isolated individuals. The Bonaventure River population is more heterogeneous than the other four because of hybridization with *A. novi-belgii* (Brouillet and Labrecque, 1987). No plantlets were observed during our August 1988 visit, but it must be remembered that asters are capable of flowering within their first year. Table 2 gives an estimate of the sizes of the populations relocated in 1988.

Flowering occurs from late July to September. Achenes were not observed during our visit in August as we were too early in the season; however, the species was able to invade locally disturbed habitat (such as roadsides) near established populations, indicating an ability of the species to perpetuate itself by seed.

Autecological data on *Aster anticostensis* are virtually non-existent. In our August 1988 visit, however, we recorded two neg-

ative interactions with other species. *Aster anticostensis* is apparently unable to hold its own against adventitious plants in an environment that is not regularly disturbed. In the Somerville population, the three individuals were practically buried among a multitude of weeds such as *Phalaris arundinacea* L., *Arctium lappa* L., *Melilotus alba* Desr. and *Trifolium* spp. When *Aster anticostensis* grows with *Aster cordifolius, A. ciliolatus* Lindley *in* DC., and especially *A. novi-belgii,* hybrids may be produced. It is interesting to note that *A. anticostensis* and *A. novi-belgii* generally do not grow in the same area. Human disturbances may, however, favor production of hybrids (as on the Bonaventure River) which are morphologically and cytologically intermediate between the two parents (Brouillet and Labrecque, 1987). Their presence on a large scale may eventually interfere with the genetic integrity of *A. anticostensis* populations.

## THREATS TO SURVIVAL

The main threats to survival of populations of *Aster anticostensis* come from disruption of river banks as a result of human activity and from regulation of water flows and levels due to dam construction.

Two sites were disturbed by human activities. At the Bonaventure River site, we observed a fair amount of traffic by four-wheel-drive vehicles. The approaches to the bridge, in particular, have been subjected to considerable compaction by heavy equipment and were rendered bare of all vegetation. In addition, cottages are being built along the river, and the riverside forest is being cut. Since our visits of 1981 and August 1985, the site has been seriously degraded, and several clones of *Aster anticostensis* that existed then have since been destroyed. Theoretically, none of these activities are allowed, but no control appears to be exerted. These disruptions may have allowed *A. novi-belgii* to infiltrate the *A. anticostensis* population, leading to the production of hybrids.

There are similar, but less serious signs of disruption at the Grande Rivière site. The main problem there is passage of all-terrain vehicles, particularly near the new pumping station; construction of this station rendered access to the strands easier. Development projects along rivers in the area are certain to harm *Aster anticostensis* populations. While other sites in Quebec do

not seem to be under threat in the short term, their existence must be made known to competent authorities to prevent eventual disruptions.

The success of populations of *Aster anticostensis* seems to depend on the cyclical disturbances caused by springtime floods. When there is little or no rise in the water level, shrub cover or *Phalaris arundinacea* takes over the habitat and pioneer species such as *A. anticostensis* may be crowded out.

This phenomenon was observed on the Saint John River, N.B., where several dams regulate the river's water level, especially on its lower course. The dams are located at Grand Falls, Beechwood and Mactaquac (H. Hinds, pers. comm., 1988). The reservoir level of the Mactaquac dam has recently (1988) been raised from 130 to 133 meters, possibly affecting the only re-localized locality of *Aster anticostensis* in New Brunswick. The only cyclical disturbances that now occur in this area are due to the drawdown of surplus water in the spring. According to Harold Hinds, this artificial phenomenon helps to preserve the habitat of several riparian species. At the Somerville site, however, the banks have a much denser vegetative cover than the Quebec sites. Most of the dominant species are aggressive weeds, and there are few *A. anticostensis* individuals left, more or less suffocated by the adventives. As with *Pedicularis furbishiae,* dams appear to break the equilibrium of cyclical disturbances that is needed to maintain the habitat (Gawler and Waller, 1987).

At the present time, the Quebec sites are not affected by this problem. It is possible that the Fort Fairfield, Maine, site was destroyed by dam construction, although our visit at that site was too brief to ascertain the status of the population with any confidence. A dam would either destroy or at least seriously affect populations of *A. anticostensis* by eliminating the disturbance cycle.

## TAXONOMY

Until recently *Aster anticostensis* was a poorly understood taxon known solely from the type specimen (Fernald, 1915, 1950; Figure 4). After examination of the type of *A. anticostensis,* it was concluded that this taxon is identical to *A. gaspensis* Marie-Victorin, described in 1932 (Figure 5). The name *A. anticostensis* thus has priority. A discussion of pertinent taxonomic literature concern-

Figure 4. Type of *Aster anticostensis* Fernald (GH).
Figure 5. Type of *Aster gaspensis* Marie-Victorin (MT).

ing *A. anticostensis* is given in Brouillet and Labrecque (1987). The exact nomenclature of the species is:

**Aster anticostensis** Fernald, Rhodora 17: 16–17, 1915. TYPE: "Québec, Anticosti, Jupiter River; River banks and grassy slopes," 22/07/1880, *J. Macoun no. 6* (as *A. paniculatus*) (HOLOTYPE, GH!).

*A. gaspensis* Marie-Victorin, Contr. Lab. Bot. Univ. Montréal 20: 3, 1932. TYPE: "Québec, sur les bords de la rivière Bonaventure, près du pont à environ 8 milles de l'embrouchure," 31/07/1931, *Marie-Victorin, Rolland-Germain & E. Jacques 37742* (HOLOTYPE, MT!).

*A. gaspensis* f. *albiflora* Marie-Victorin, Naturaliste Canadien 71: 209, 1944. TYPE: "Platières caillouteuses vers le hutième mille," *Marie-Victorin, Boivin, Raymond & Kucyniak 4035* (HOLOTYPE, MT!).

*A. hesperius* Gray var. *gaspensis* (Vict.) Boivin, Phytologia 23: 34, 1972.

*A. hesperius* Gray var. *gaspensis* (Vict.) Boivin f. *albiflora* (Vict.) Boivin, Phytologia 23: 35, 1972.

*Aster anticostensis* may be mistaken for *A. novi-belgii, A. borealis* and *A.* "*longifolius*" (*sensu* Semple and Heard, 1987). The latter is a still poorly known taxon found mainly in northern

Ontario and Quebec, south to Wisconsin (Semple and Heard, 1987; Semple et al., 1983). Although they are allopatric, *A. anticostensis* and *A.* "*longifolius*" share the same number of chromosomes ($2n = 80$ and 64). However, they may be distinguished by their leaves (coriaceous in the case of *A. anticostensis,* thinner in *A.* "*longifolius*"); the shape of the inflorescence (panicle long and narrow in *A. anticostensis,* more open in *A.* "*longifolius*"); and the habitat of each (humid depressions in the case of *A.* "*longifolius*," whereas *A. anticostensis* favors calcareous upper beaches). The relationships of *A.* "*longifolius*" remain to be established.

The species has not been described completely before. A description is thus provided here. Diagnostic characters are emphasized.

Perennial, propagating by *long stoloniferous rhizomes forming loose clones; stems* 25–75 cm tall, 2–4 mm in diameter, *stiff, erect,* grooved, puberulent along the lines of decurrence of the leaves, especially towards apex, stem branches ramified toward the top; *the upper lateral branches strongly ascending; leaves sessile, linear or linear-lanceolate, coriaceous,* 9–16 cm long, 5–18 mm wide, *ascending,* slightly narrower and clasping at the base, the apices acute, *entire to subentire,* with midveins prominent beneath; margins scabrous; rameal leaves reduced, 8–50 mm long, 1.5–5 mm wide; *capitulescence* paniculiform, *loose, elongate, consisting of* 11–51 *large, single heads at the ends of the primary and secondary branches*; peduncles long, 8–57 mm; heads with involucres 6–10 mm long; outer involucral bracts 3.3–5.9 mm long, 0.8–1.2 mm wide; inner 4.8–7.0 mm long, 0.9–1.1 mm wide; involucral bracts foliaceous, in 2 or 3 unequal series; rays 25–44, 9.5–20 mm long, pale purple, lilac or sometimes white; disc florets 29–52, yellow becoming reddish with age, corolla lobes erect, comprising 15–20% of the limb; pappus bristles as long or slightly longer than corolla; cypselas sparsely puberulent, mostly on the ribs, 1–1.5 mm long; chromosome number: $2n = 80$.

The following key distinguishes *Aster anticostensis* from related taxa.

1. Plant slender; rhizomes filiform, less than 2 mm in diameter; leaves linear, recurved at the margins, sessile, non-clasping; large but few heads (often monocephalous) on very slender peduncles ..... *A. borealis*

1. Plant robust; rhizomes thick, more than 2 mm in diameter; leaves different; plant usually not monocephalous ..... 2
   2. Leaves oblanceolate, slightly fleshy, clasping base; capitulescence highly branched, numerous heads on short (usually less than 3 cm) peduncles ..... *A. novi-belgii*
   2. Leaves linear-lanceolate, little or not narrowing at the base, sessile or almost sessile; capitulescence paniculiform, open, heads borne on long (usually more than 3 cm) peduncles ..... 3
      3. Leaves arched, coriaceous, rigid, persisting; capitulescence made of strongly ascending branches ..... *A. anticostensis*
      3. Leaves slightly fleshy, not rigid, deciduous at the base at anthesis; capitulescence branches not strongly ascending ..... *A.* "*longifolius*"

## STATUS

*Aster anticostensis* is not included in the lists of rare plants of Québec (Bouchard et al., 1983), New Brunswick (Hinds, 1985), or Maine (Dibble et al., 1989). Since *A. anticostensis* populations are few in number and have a limited range of distribution, we suggest giving the taxon a "threatened" status, with a Nature Conservancy ranking of G2 for the global range, N2 for Canada, and S2 for the Province of Québec. However, the situation is different in New Brunswick where, as long as no further populations are located, the species must be considered as "endangered," with an S1 ranking. In Maine, where the taxon was last collected in 1901, the status "historically present" must be given.

The species must be looked for in its critical habitat, particularly in New Brunswick and Maine, where its survival is precarious, and most carefully searched for along the St. John and Aroostook Rivers where it was known historically. Similarly, searches should be made on Anticosti Island and along rivers of the Baie des Chaleurs area (Québec and New Brunswick). Extant populations should be monitored, and their ecology and resilience investigated.

SPECIMENS EXAMINED. [The list does not include those specimens cited under *Aster gaspensis* by Brouillet and Labrecque (1987).]

CANADA. **Québec.** Bonaventure Co.: Bonaventure River, near the bridge of the St. Elzéar road, *J. Labrecque, L. Brouillet & D. Whetstone 99,* 23/08/1988 (MT); Petit-Pabos River, eroded bank at about 3 km from the mouth, *JL, LB & DW 184,* 25/08/1988 (MT). Gaspé-est Co.: Grande-Rivière River, calcareous bank about 5 km from the mouth, *JL, LB & DW 132, 162,* 24/08/1988 (MT). Matapédia Co.: Restigouche River, 4 km southwest of Matapédia, *JL, LB & DW 64,* 23/08/1988 (MT). **New Brunswick.** Carleton Co.: Somerville, about 1.6 km south of Hartland covered bridge on the St. John River, *JL, LB & DW 3,* 22/08/1988 (MT); *H. Hinds & S. Clayden 68,* 21/08/1977 (as *A. novi-belgii*) (UNB); Woodstock, gravelly flat along an island in the St. John River, *W. G. Dore & E. Gorham 45-880,* 28/07/1945 (as *A. foliaceus*) (DAO, MT).

U.S.A. **Maine**. Aroostook Co.: Fort Fairfield, gravelly bank of the Aroostook River, *E. F. Williams, B. L. Robinson & M. L. Fernald, s.n.,* 15/08/1901 (as *A. junceus*) (ISC, GH, MT, WIS); *J. R. Churchill, s.n.,* 11 & 16/08/1901 (as *A. junceus*) (MO).

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# VASCULAR FLORA OF THE WETLAND AND PRAIRIE COMMUNITIES OF GAVIN BOG AND PRAIRIE NATURE PRESERVE, LAKE COUNTY, ILLINOIS

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## ABSTRACT

The vascular flora of the wetland and graminoid plant communities at Gavin Bog and Prairie Nature Preserve in Lake County, Illinois, is described. A total of 246 vascular plant species and three hybrids was found in four broad community classes: bog, marsh, sedge meadow, and prairie. Three bog communities, low-shrub zone, tall-shrub zone, and forested-bog zone, were recognized. The prairie primarily includes wet prairie and mesic prairie. Fifteen threatened or endangered plant species for Illinois were recorded from the nature preserve including two, *Carex brunnescens* and *Vaccinium oxycoccos*, not accurately reported from Illinois before this study.

Gavin Bog is an oligotrophic acid peatland in an advanced developmental stage. Although the two major plant families characteristic of acid peatlands in the Great Lakes region, Cyperaceae and Ericaceae, are also the best-represented families at Gavin Bog, little compositional similarity exists between Gavin Bog and marsh and other bog/marsh communities in Lake County, Illinois.

A total of 5.7% of the vascular flora at Gavin Bog and Prairie Nature Preserve is alien to North America. One exotic species, glossy buckthorn (*Rhamnus frangula*), currently dominates the tall-shrub zone in the bog, occurs throughout the forested zone, and is threatening the low-shrub zone. The presence of this species has probably resulted in ecological shifts favoring shade-tolerant species throughout the bog. Ecological consequences of various management options are considered.


Key Words: bog, prairie, sedge meadow, marsh, *Carex canescens, Vaccinium oxycoccos, Rhamnus frangula,* fire, management, Gavin Bog and Prairie Nature Preserve, Illinois

## INTRODUCTION

Bogs are an uncommon community type in Illinois and are restricted to the Northeastern Morainal Natural Division (Schwegman, 1973). Twelve bogs, including Gavin Bog, were identified by the Illinois Natural Areas Inventory (INAI) as significant natural features (White, 1978). These bogs, representing four natural communities (graminoid-bog, low-shrub, tall-shrub, and forested-bog), contain a distinctive flora that includes many

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boreal species at the southern limits of their Midwestern ranges. Consequently, numerous bog species are rare in the state, and several are listed as Threatened or Endangered in Illinois (Sheviak, 1981). With the exception of Volo Bog, the only Illinois bog containing the classic floating herb mat surrounding an open water pond (Sheviak and Haney, 1973), the vegetational composition of Illinois bogs has been poorly documented. Early accounts of the vegetation of several Illinois bogs were given by Waterman (1921, 1923, 1926) and Wascher (1934, M.S. thesis, University of Illinois, Champaign–Urbana). Voss (1934) described the Pleistocene vegetation of several Illinois and other Midwestern bogs through pollen analysis. The paucity of contemporary vegetation descriptions for Illinois bogs prompted the present study in which we document the vegetation composition of wetland and prairie communities at Gavin Bog and Prairie Nature Preserve.

## STUDY AREA

Gavin Bog and Prairie Nature Preserve contains an oligotrophic peatland (Johnson, 1985), or bog, surrounded by emergent wetland, prairie, and forest communities. Upland forest communities were not included in this floristic study. The nature preserve lies 2 km (1.3 miles) east of Fox Lake in Lake County, Illinois (Figure 1), and encompasses 55 hectares (136.5 acres). A dedicated Illinois Nature Preserve, the area is owned and managed by the Lake County Forest Preserve District.

Gavin Bog and Prairie Nature Preserve lies in a depression on the western edge of the Valparaiso Moraine, a Wisconsinan-age end moraine (Willman, 1971). Part of the area occurs on Wadsworth till of the Wedron formation, a till of mainly clay and silty clay (Willman, 1971; Lineback, 1979). The bog is underlain by Grayslake Peat, a peat deposit containing some organic silts that formed on former lake basins (Willman, 1971). Houghton muck soil is found in the bog and in parts of the marsh and prairie; Peotone silty clay loam soil underlies sedge meadow, marsh and prairie vegetation. Both soils are very poorly drained and formed on level or depressional sites (Paschke and Alexander, 1970).

The preserve has been managed by the Lake County Forest Preserve District since 1977, and the prairie was burned annually in the spring until 1983. Since that time, management fires have been conducted in alternate years, and brush has been removed.

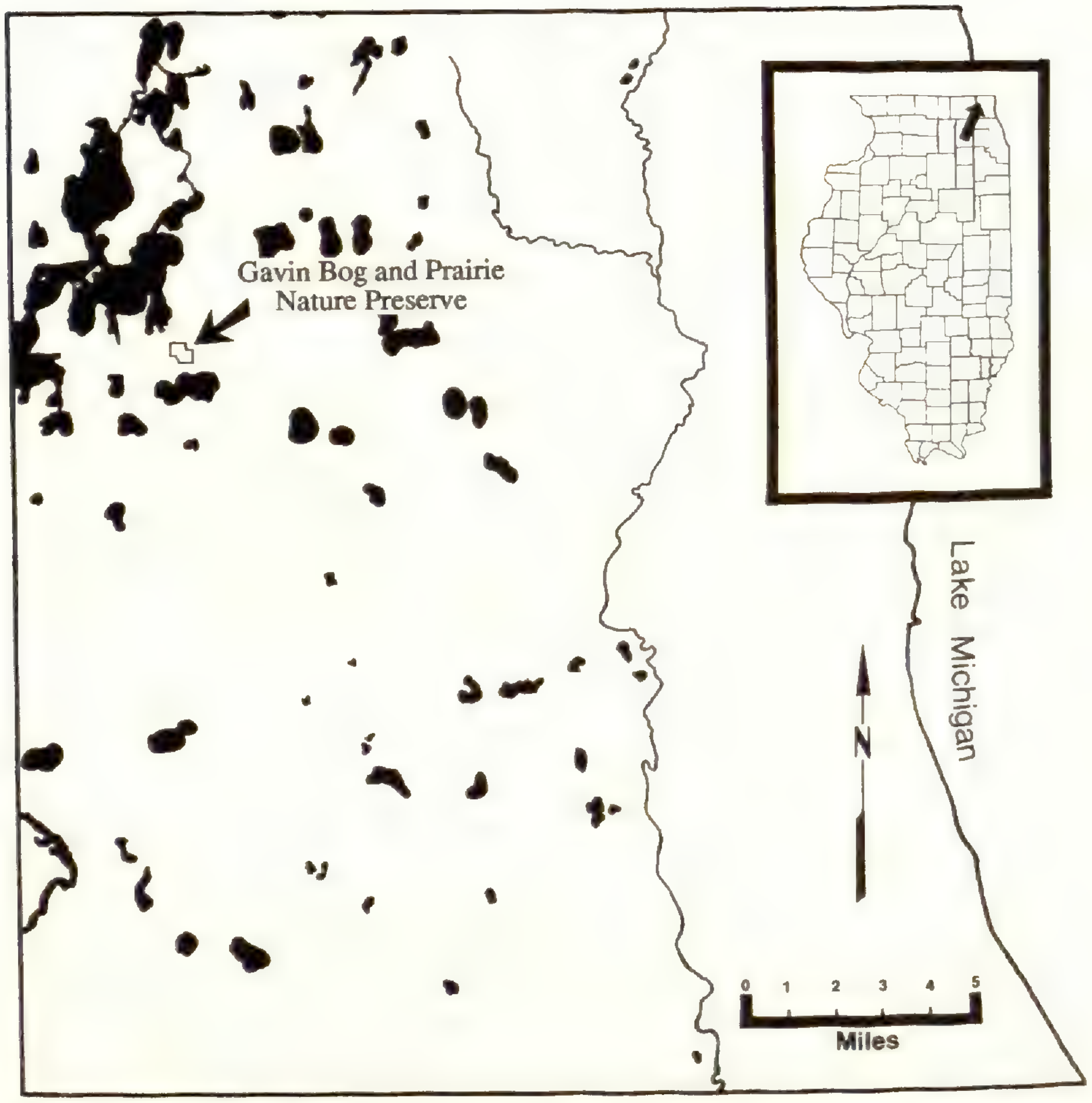


Figure 1. Location of Gavin Bog and Prairie Nature Preserve in Lake County, Illinois. Lakes and the principal rivers are shown in black.

Past disturbances include cattle grazing in the bog prior to 1960, and attempts at draining some of the wetlands. A drainage ditch adjoining the prairie was filled in 1984.

## METHODS

Seven site visits were made to the study area between July 1985 and May 1989. At these times, species were noted and their habitats and relative abundance (e.g., abundant, common, occasional, uncommon, rare) were estimated. All communities were visited in spring, summer, and autumn. Natural communities were classified following White (1978). Collections were made of species that could not be field identified or were state records; these are

deposited in ILLS. The nomenclature and phylogenetic order used in the checklist of species (Appendix) follow Mohlenbrock (1986), with the exception of two species unreported from the state prior to 1986; in those instances, nomenclature follows Swink and Wilhelm (1979).

Sorensen's Index of Similarity (Mueller-Dombois and Ellenberg, 1974) was used to compare species occurring in the marsh and bog communities at Gavin Bog (115 species) with those on species lists compiled for three other Illinois bogs and one Indiana bog that also include marsh vegetation. Marsh communities were included because in some cases the bog/marsh border is poorly defined. The four other sites were Wauconda Bog (136 species), list compiled by Robert Evers, Galen Smith, Gerald Paulson, Floyd Swink, Michael Madany, Keith Wilson, and Robbin Moran between 1947 and 1977 (Illinois Natural History Survey and INAI files); Volo Bog (106 species), list compiled during intensive sampling by Charles Sheviak and Alan Haney (1973); Barrington Bog (75 species, including sedge meadow), list compiled by Wayne Schennum (Illinois Nature Preserve Commission files); and Pinhook Bog (168 species) in La Porte County, Indiana, list compiled by Gerould Wilhelm with Marlin Bowles, James Aldrich, Ken Dritz, Norm Henderson, Craig Johnson, and Elizabeth Shimp from 1979 through 1988 (Wilhelm, 1980).

To date the dominant woody vegetation in the bog, the age of a selected tamarack (*Larix laricina* (DuRoi) K. Koch) was estimated by counting growth increments of a core removed with an increment borer. The age of an individual glossy buckthorn (*Rhamnus frangula* L.) was estimated from growth increments on a basal stem segment removed with a hack saw.

## RESULTS AND DISCUSSION

### Community Descriptions

Seven wetland and prairie plant communities occur at Gavin Bog and Prairie Nature Preserve: forested bog, tall-shrub bog, low-shrub bog, marsh, sedge meadow, wet prairie, and mesic prairie. Species composition, with relative abundance estimates and the associated plant communities, is compiled in the Appendix.

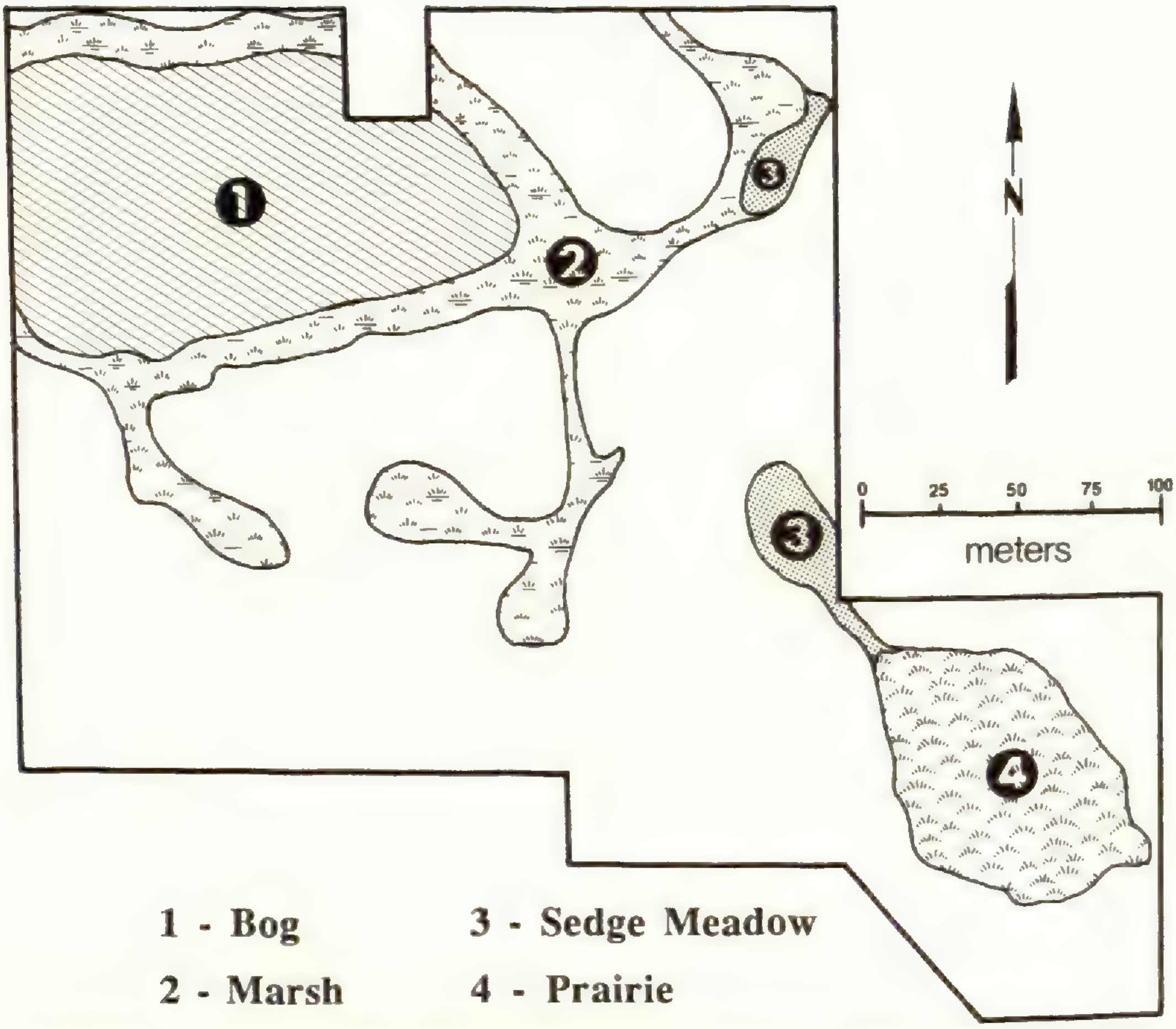


Figure 2. Wetland and prairie plant communities of Gavin Bog and Prairie Nature Preserve, Lake County, Illinois.

The bog communities contain a central ellipse of forested bog bordered by a broad, concentric band of tall-shrub bog. A small low-shrub bog community occurs near the north-central edge of the forested bog. The open water pool and floating herb mat characteristic of many bogs with earlier successional stages (Sheviak and Haney, 1973; Johnson, 1985) are absent from Gavin Bog. The depression containing Gavin Bog was completely peat-filled before 1934 (Voss, 1934). A marsh community borders the tall-shrub bog as a concentric ring, with narrow lobes formed to the south and east. A sedge meadow borders the east lobe of the marsh. A second sedge meadow and wet and mesic prairie communities occur to the south-southeast. These latter graminoid communities are separated from the bog and marsh by successional fields and upland forest (Figure 2).

Bog Communities. Hummocks colonized by the mosses *Sphagnum* spp. (including *S. centrale* C. Jens.), *Aulacomnium*

*palustre* (Hedw.) Schwaegr., and *Calliergon* sp. characterize all bog communities. The forested bog is dominated by *Larix laricina* in the canopy. This species was present in the early 1930's (Voss, 1934). A core from an increment borer of one of the largest individuals in the bog today (18 cm dbh) had about 61 growth increments. This finding suggests that tamaracks probably persisted at the site despite a pathological infestation of bark beetles on tamarack in the region (Shelford, 1963). A dense understory of the exotic shrub *Rhamnus frangula* occurs throughout the forested zone. The native shrubs *Ilex verticillata* (L.) Gray, *Vaccinium corymbosum* L., and *Gaylussacia baccata* (Wang.) K. Koch are occasional to common; *Vaccinium myrtilloides* Michx. is uncommon and *Ribes hirtellum* Michx. is rare. Common-to-occasional groundcover species are *Carex brunnescens* (Pers.) Poir. var. *sphaerostachya* (Tuckerm.) Kukenth., *Carex trisperma* Dew., and *Trientalis borealis* Raf. The tall-shrub bog is a dense, nearly impenetrable, zone dominated by *Rhamnus frangula* with *Ilex verticillata* common to occasional and *Aronia melanocarpa* (Michx.) Ell. locally common. *Betula pumila* L. is present but rare. Herbaceous species include *Carex trisperma, C. brunnescens, Dulichium arundinaceum* (L.) Britt., *Osmunda cinnamomea* L., *O. regalis* L., and the exotic *Lythrum salicaria* L. The low-shrub bog forms a distinctive zone characterized by dense *Chamaedaphne calyculata* intermixed with *Gaylussacia baccata, Rhamnus frangula, Eriophorum virginicum* L., *Carex trisperma,* and *Vaccinium oxycoccos* L., a species previously unverified from Illinois (*see* section on state-listed plant species).

In May 1989, several white oak (*Quercus alba* L.) seedlings were observed on *Sphagnum*-covered hummocks throughout the forested-bog zone. These hummocks were drying out in May 1989, and water levels in the bog were the lowest observed since 1985 when this study began. We believe the appearance of the oak seedlings is a response to a drought-induced lowering of the water table and not an indication of succession toward a more mesophytic forest community. Gavin Bog, like Volo Bog (Sheviak and Haney, 1973), provided no salient evidence of change toward a more mesophytic forest community, despite its advanced stage of development.

A few characteristic bog species that we did not find are reported from Gavin Bog (Broulliard, Lake County Forest Preserve District, pers. comm.). These include *Toxicodendron vernix* (L.)

Kuntze, *Rhamnus alnifolia* L'Her., and *Sarracenia purpurea* L. (observed in 1974 by Charles Sheviak, INAI files). *Andromeda glaucophylla* Link was collected from a "cranberry marsh, [in] open places in tamarack swamp" by E. J. Hill in 1908 in Grant Township. This site may have been Gavin Bog since other Hill collections with similar site descriptions include taxa known or formerly known from Gavin Bog, also in Grant Township. These taxa, if still present, occur at low population levels.

MARSH COMMUNITY. *Typha latifolia* L. strongly dominates the marsh. *Sium suave* Walt. and the introduced species *Lythrum salicaria* (purple loosestrife) and *Solanum dulcamara* L. are common. Purple loosestrife has not yet reached the alarming densities found in similar wetland sites in northeastern Illinois. Common-to-occasional associates include *Acorus americanus* (Raf.) Raf., *Carex scoparia* Schkuhr, *Carex lanuginosa* Michx., *Eleocharis erythropoda* Steud., *Equisetum fluviatile* L., *Lysimachia thyrsiflora* L., *Lycopus uniflorus* Michx., *Phalaris arundinacea* L., *Polygonum amphibium* L., and *Sparganium eurycarpum* Engelm. *Veronica scutellata* L. is present, but rare.

SEDGE MEADOW. The sedge meadow is characterized by a wide variety of graminoid species. The dominant sedge and grasses are *Carex stricta* Lam., *Calamagrostis canadensis* (Michx.) Beauv., and *Spartina pectinata* Link; common-to-occasional species include *Carex buxbaumii* Wahlenb., *C. festucacea* Schkuhr, *C. lacustris* Willd., *Glyceria striata* (Lam.) Hitchc., *Scirpus acutus* Muhl., and *Iris shrevei* Small. The State-threatened sedge *C. atherodes* Spreng., a species that superficially resembles *C. lacustris,* is reported to be common in this community (Bowles, 1988; unpublished report, Morton Arboretum, Lisle, IL). Although no dicot herbs are dominant here, many characteristic species are present, including *Asclepias incarnata* L., *Campanula aparinoides* Pursh., *Galium boreale* L., *Lathyrus palustris* L., and *Ranunculus flabellaris* Raf.

PRAIRIE COMMUNITIES. Wet prairie occurs in slightly depressed parts of the prairie and mesic prairie occurs on slightly elevated sites. Dominant species in the wet prairie are *Calamagrostis canadensis, Carex stricta,* and *Spartina pectinata.* Associates include *Aster simplex* Willd., *Saxifraga pensylvanica* L., *Spiraea alba* DuRoi, *Stachys palustris* L., and *Veronicastrum virginicum* (L.)

Farw. The mesic prairie has a greater abundance and diversity of dicot herbs than the wet prairie. Characteristic species of the mesic prairie are *Andropogon gerardii* Vitman, *Aster novae-angliae* L., *Castilleja coccinea* Spreng., *Comandra umbellata* (L.) Nutt., *Dodecatheon meadia* L., *Liatris pycnostachya* Michx., *Phlox pilosa* L., *Silphium terebinthinaceum* Jacq., *Solidago riddellii* Frank, *Sorghastrum nutans* (L.) Nash, and *Zizia aurea* (L.) Koch.

The Illinois Natural Areas Inventory file on Gavin Bog indicates that a fen community is present; however, several indicator species of calcareous fens (the only fen type identified in Illinois by the INAI) appear to be absent from the study area: *Cirsium muticum* Michx., *Gentiana procera* Holm, *Parnassia glauca* Raf., *Pedicularis lanecolata* Michx., *Potentilla fruticosa* L., and *Solidago ohiensis* Riddell. The apparently erroneous report of this interesting community type in the study area is probably due to the presence of *Cypripedium candidum* Muhl. in the mesic prairie, a species that is sometimes found in (but not restricted to) calcareous fens.

The prairie as a whole, about 2.6 hectares (6.4 acres), has the greatest diversity of the communities studied, with 140 vascular plant taxa. The species numbers found in the other community classes studied are less than half this number. Sixty-six species were recorded from the forested, tall-shrub, and low-shrub bog communities in an area of about 7 hectares (17.5 acres). Sixty-seven species were recorded from the marsh in an area of approximately 5.9 hectares (14.5 acres) and 67 species were recorded from the sedge meadow in an area totalling about 0.7 hectares (1.7 acres).

Similarity Indices. The Sorensen's similarity indices compiled for bog and adjoining marsh communities at four Illinois bogs and one Indiana bog (Pinhook Bog) are summarized in Table 1. Despite certain weaknesses of such comparisons (e.g., the thoroughness of the reports may vary, lists were compiled at different times), they do indicate a surprisingly low vegetational similarity between the four Illinois sites, all occurring within 18.75 km (11.5 miles) of Gavin Bog. These data conflict with Curtis's suggestion (1959, p. 240) that the vegetation composition of bogs (conifer swamps) in close proximity are often very similar. His assessment appears to have been based only on a comparison of characteristic species found in bogs and not on total species composition. For

Table 1. Sorensen's similarity indices calculated for four Lake County, Illinois bogs and one Indiana bog (Pinhook). Marsh communities were included in the comparisons. Numbers represent % of floristic elements in common.

| | Pinhook | Wauconda | Barrington | Volo |
|---|---|---|---|---|
| Gavin | 39 | 39 | 31 | 41 |
| Volo | 36 | 45 | 35 | |
| Barrington | 32 | 33 | | |
| Wauconda | 30 | | | |

instance, he reported that similarity values for bogs in Wisconsin, Minnesota, Michigan, and Illinois are over 80%; however, the Illinois data on which that comparison is based (Waterman, 1923) provide only a brief listing of species and these are primarily restricted to bogs. A comparison of a selected few characteristic bog species from the four Illinois communities reviewed above would yield a much higher similarity index than was achieved by comparing total species lists. Nevertheless, the most important plant families in Wisconsin bogs, Cyperaceae and Ericaceae (Curtis, 1959), are also the best represented plant families at Gavin Bog: 8 species of Cyperaceae and 5 species of Ericaceae.

One explanation for the low similarity indices between these plant communities can be traced to the wide use of the term "bog." Illinois bogs are originally calcareous and only later become acidic (Sheviak, 1974). Because acids are normally flushed away by moving water, acidification occurs in basins with weak or no outlets. These sites are characterized by *Sphagnum*-covered hummocks and include an Ericaceous shrub component. All bogs in Illinois are oligotrophic peatlands; they receive water from geogenous sources as well as from precipitation. Shallow basins on gentle gradients with hydrologic outlets can also form oligotrophic peatlands but do not become strongly acidic because moving water prevents a build-up of acids (Johnson, 1985). In Illinois, these sites are not colonized by *Sphagnum* spp., contain few if any Ericaceous shrubs, and probably remain calcareous with a nearly neutral pH. Wauconda Bog and Barrington Bog belong to this latter category, perhaps more appropriately classified as minerotrophic peatlands, or fen and marsh complexes. Wauconda Bog is forested with tamaracks and yellow birch and thus should be referred to as a forested fen (M. L. Bowles, pers. comm.). This distinction between oligotrophic peatlands in Illinois does not, however, explain the dissimilarity between the acid peatlands in

Table 2. Illinois Threatened and Endangered plants (Sheviak, 1981; Illinois Endangered Species Protection Board, 1989) found at Gavin Bog and Prairie Nature Preserve, Lake County, Illinois.

| Species | Status in Illinois | Habitat |
|---|---|---|
| *Agropyron trachycaulum* (Link) Malte. var. *unilaterale* (Vasey) Malte. | E | mesic prairie |
| *Carex brunnescens* (Pers.) Poir. var. *sphaerostachya* (Tuckerm.) Kukenth. | E | forested bog, tall-shrub bog |
| *Carex atherodes* Spreng. | T | sedge meadow |
| *Carex trisperma* Dew. | E | low-shrub bog, tall-shrub bog, forested bog |
| *Chamaedaphne calyculata* (L.) Moench | T | low-shrub bog, forested-bog edge |
| *Cypripedium candidum* Muhl. | E | mesic prairie |
| *Cypripedium parviflorum* Salisb. | E | mesic prairie |
| *Eriophorum virginicum* L. | E | low-shrub bog |
| *Larix laricina* (DuRoi) K. Koch | T | forested bog |
| *Oenothera perennis* L. | E | old field |
| *Ribes hirtellum* Michx. | E | forested-bog edge |
| *Trientalis borealis* Raf. | T | forested bog, tall-shrub bog |
| *Vaccinium corymbosum* L. | E | forested bog, tall-shrub bog |
| *Vaccinium oxycoccos* L. | E | low-shrub bog, forested-bog edge |
| *Veronica scutellata* L. | T | marsh |

Table 1 (Gavin, Volo, and Pinhook Bogs). We speculate that these differences are related to the individual disturbance histories of the sites, the fluctuation of water levels, and, with Pinhook Bog, phytogeographic separation.

## State-listed Threatened and Endangered Plant Species

Ten Illinois Endangered and four Illinois Threatened species (taxa) were recorded from the Gavin Bog and Prairie Nature Preserve during this study (Table 2). An additional Illinois Threatened species, *Carex atherodes* Spreng., is reported from the sedge meadow (Bowles, 1988; unpubl. report, Morton Arboretum, Lisle, IL). Two species of the bog community, *Carex brunnescens*

var. *sphaerostachya* (Taft and Solecki, 1987) and *Vaccinium oxycoccos,* have not previously been included as members of the Illinois flora (Jones, 1963; Swink and Wilhelm, 1979; Mohlenbrock, 1986). An earlier collection of a specimen labelled *Carex brunnescens* (*Evers 10338 & Evers 10342,* ILLS) from nearby Volo Bog is actually *Carex canescens* L. var. *disjuncta* Fern., a species closely resembling *C. brunnescens,* which is also previously unreported for Illinois. *C. canescens* var. *disjuncta* is still present at Volo Bog, where it is surprisingly common in the forested bog zone (*Taft & Solecki 2322, Taft & Solecki 2323,* ILLS).

*Vaccinium oxycoccos* L., the small cranberry, has not been previously verified from Illinois. This species occurs in bogs and peatlands from Greenland and across northern North America to Alaska and south to West Virginia, Ohio, Wisconsin, Minnesota, Washington, and California (Fernald, 1950; Gleason, 1952). At Gavin Bog, it was locally common in the low-shrub bog and occasional at the transition zone between low-shrub bog and forested bog during the first two years of this study; however, we observed a marked reduction in the population during the last year of this study. Where formerly this trailing, slender-stemmed shrub had been frequent, growing interlaced with *Sphagnum* spp. on hummocks beneath *Chamaedaphne calyculata,* in 1989 only a few stems were observed, and these were among dead stems on dry hummocks. This reduction may be attributable to the 1988 drought. The population was mainly vegetative, and only a few flowering stems were seen during this study (*Taft & Solecki 2238, Taft & Solecki 2239,* ILLS). A vegetative specimen labelled *V. macrocarpon* was collected from Gavin Bog in 1971 (*Sheviak 569,* ILLS), but this material may actually be *V. oxycoccos.* Illinois Natural Areas Inventory (White, 1978) field data sheets report *V. macrocarpon* from Cedar Lake Bog and from Gavin Bog, but these determinations may have been based on vegetative material because these species flower infrequently in Illinois and the two taxa are difficult to distinguish vegetatively. *V. macrocarpon* may also be present at Gavin Bog in a vegetative condition, but until flowering material can be documented, this population should be referred to as *V. oxycoccos.*

The small cranberry has been reported twice before from Illinois (Waterman, 1926; Wascher, 1934, M.S. thesis, University of Illinois, Champaign–Urbana). Wascher (1934, M.S. thesis, University of Illinois, Champaign–Urbana) lists *V. oxycoccos*

among 67 species of Illinois peat bogs. His inclusion of *Vaccinium oxycoccos* is questionable since he did not cite and apparently did not collect a voucher specimen and gives no specific location information other than peat bogs in Illinois. Furthermore, his list does not include *V. macrocarpon,* a State-endangered species known from four or five Illinois bogs (Sheviak, 1981). Waterman (1926) reported *V. oxycoccos* from a floating mat at Cedar Lake Bog in Lake County; however, no voucher specimen is referenced. Further, there is a specimen of *V. macrocarpon* (*Evers 4634,* ILLS) from Cedar Lake Bog.

*Vaccinium oxycoccos* is regarded as an allotetraploid species that arose by hybridization between *V. macrocarpon* and *V. microcarpum* (Turcz.) Hook., and specimens of *V. oxycoccos* with characteristics of one of the former parents are frequently found (Gleason, 1952; Wood, 1961). One specimen of flowering material from Gavin Bog (*Taft & Solecki 2239,* ILLS) has a pair of large (3.7 and 3.5 mm long), greenish bracts on one pedicel, a characteristic of *V. macrocarpon*; however, an adjacent pedicel on the same plant has small (1.6 and 1.7 mm long), pale yellow bracts typical of *V. oxycoccos.* The bracts are attached at or below the middle on both pedicels, a characteristic of *V. oxycoccos.* Furthermore, the pedicels on both flowering specimens range in length from 4 to 6 cm. The pedicels for *V. macrocarpon* are typically 1 to 3 cm long (Gleason, 1952; pers. obs.). Other vegetative and flower characteristics correspond with *V. oxycoccos. Taft & Solecki 2238* is typical *Vaccinium oxycoccos.*

*Vaccinium oxycoccos* and *Carex brunnescens* var. *sphaerostachya* were recently listed by the Illinois Endangered Species Protection Board as endangered in Illinois (Illinois Endangered Species Protection Board, 1989). *Carex canescens* var. *disjuncta* has been proposed for listing as endangered in the State in 1990 (Illinois Endangered Species Protection Board, unpubl. memo., 1989).

## Taxonomic Summary

Three hybrids and 245 plant species representing 68 families and 158 genera were identified in the wetland and prairie communities at Gavin Bog and Prairie Nature Preserve (Appendix). The major plant groups were represented as follows: 10 vascular cryptogams, 1 gymnosperm, 72 monocotyledons, and 165 dicotyledons. The three largest plant families were the Cyperaceae and

Asteraceae, each with 34 species, and the Poaceae with 20 species. *Carex* was the largest genus, represented by 22 species. Fourteen species of vascular plants recorded during this study (5.7% of the total) are alien to North America (Swink and Wilhelm, 1979).

## Ecological and Management Considerations for the Bog Communities

The prairie has been managed using controlled fire and brush cutting with excellent results since 1977. Prior to management, the suppression of fire had resulted in the encroachment of woody plants throughout much of the prairie (Broulliard, pers. comm.). Now, shrubs have been reduced to scattered individuals and occasional small thickets. No management has occurred in the sedge meadow, marsh, or bog communities. The exotic shrub *Rhamnus frangula* (glossy buckthorn) with occasional *Ilex verticillata* form dense, nearly impenetrable, thickets throughout the tall-shrub and forested-bog zones. Glossy buckthorn was first recorded in Illinois in 1912, where it was found well established in Cook County (Sherff, 1912). By 1955, this Eurasian species was known from five primarily northeastern Illinois counties, including Lake County (Jones and Fuller, 1955). By 1978, it was known from 18 counties (Mohlenbrock and Ladd, 1978). European starlings are strongly implicated as the primary dispersal agent (Howell and Blackwell, 1977). Because the fruits of this species can float for several weeks (Ridley, 1930), water can also aid in dispersal.

*Rhamnus frangula* may have become established in the bog following grazing disturbance. Attempts at draining portions of the wetlands have occurred, and the water table in the bog may have been lowered at some time. A former landowner reported that Gavin Bog was much drier during the 1950's when it was grazed (Broulliard, pers. comm.). This dry period may have stressed the native tall shrubs bordering the forested-bog community and, together with grazing disturbance, created an opportunity for the establishment of the aggressive *R. frangula.* Precipitation deficits occurred in the 1950's, and seven of the eleven years from and including 1948 to 1958 had below average rainfall at Antioch, Illinois, the nearest reporting station to Gavin Bog (U.S. Department of Commerce, Weather Bureau data).

Glossy buckthorn branches profusely at the base and dead stems are often found among smaller, live stems. Because of this die-

back habit, it may be impossible to determine when buckthorn became established in the bog. One of the larger stems found, a living stem 4.5 cm in diameter at the base, had 39 growth increments. If these growth increments are annual growth rings, *Rhamnus frangula* has been in Gavin Bog at least since about 1950.

The composition of the tall-shrub zone in Illinois bogs prior to the invasion of *Rhamnus frangula* has been briefly described (Waterman, 1921, 1923, 1926). Important components included *Aronia melanocarpa, Betula pumila, Cornus stolonifera, Ilex verticillata, Toxicodendron vernix,* and *Vaccinium corymbosum.* This zone is believed to be a naturally occurring and stable community (Sheviak and Haney, 1973). The tall-shrub bog zone that existed at Gavin Bog before the invasion of *Rhamnus frangula* was probably dominated by *Ilex verticillata* with common to occasional *Aronia melanocarpa, Betula pumila, Vaccinium corymbosum,* and *Cornus stolonifera.*

Some populations of the rare species in Gavin Bog (*Vaccinium oxycoccos, V. corymbosum, V. myrtilloides, Ribes hirtellum,* and *Betula pumila*) may be limited by the shading and competitive effects of *Rhamnus frangula.* We found only single specimens of the last two species listed, both on the margin of the tall-shrub and forested-bog zone. The three *Vaccinium* species occur primarily in and adjacent to the low-shrub zone where light appears to be more available throughout the growing season. The availability of light is a controlling factor in bog community composition (Gates, 1942; Dansereau and Segadas-Vianna, 1952; Schwintzer and Williams, 1974), and in this regard, fire has been important in the vegetational composition of many more northern bogs (Gates, 1942). *Rhamnus* thickets and the tamarack-dominated canopy of the forested-bog zone shade the borders of the small low-shrub zone, which contains three Illinois Endangered plant species and one Illinois Threatened species (Table 1). We were unable to locate *Sarracenia purpurea* (Illinois Endangered), formerly reported as a single clump from the low-shrub zone (Illinois Natural Areas Inventory files). This species may have been eliminated from Gavin Bog due to increased shading. Pitcher plants, for example, have been eliminated from a Michigan bog because of increased shading (Schwintzer and Williams, 1974). The other species (*Toxicodendron vernix* and *Rhamnus alnifolia*) we did not find that were reported from the bog may also have been eliminated by competition from glossy buckthorn. The low-

shrub zone at Gavin Bog evidently was much larger than at the time of this study. In an area adjacent to the small low-shrub zone, *Chamaedaphne calyculata* is a common understory species with glossy buckthorn and tamaracks forming the overstory. The latter two species appear to have invaded a low-shrub zone dominated by *C. calyculata.* Low-shrub zones in bogs are prone to invasion by tall shrub species and tamarack, which shade and eventually eliminate the shade-intolerant low-shrub species like *C. calyculata* (Gates, 1942; Schwintzer and Williams, 1974). Glossy buckthorn is currently invading the remaining low-shrub zone at Gavin Bog. Judging from the rate of change observed in a Michigan bog where a low-shrub zone advanced to tall-shrub and forested-bog stages in just 70 years (Schwintzer and Williams, 1974), prescribed fires that eliminate or reduce the cover of tall-shrub species may be necessary to maintain low-shrub zones in bogs, particularly where low-shrub zones persist in bogs lacking open-water areas.

Species apparently favored by the shade of the tamarack and tall-shrub zone include *Carex trisperma, C. brunnescens,* and *Trientalis borealis.* These species are distributed throughout much of the forested-bog zone, while the two *Carex* species also occur throughout portions of the tall-shrub zone. Similar findings are reported for a Michigan bog (Schwintzer and Williams, 1974).

*Rhamnus frangula* readily resprouts following cutting (R. R. Heidorn 1989, Illinois Department of Conservation, pers. comm.). Efforts to control the resprouting of *R. frangula* and another exotic buckthorn species (*R. cathartica* L.) with stump-treatment herbicides have been successful without apparently disturbing adjacent vegetation (Kline, 1981; Apfelbaum, 1984; Hefty, 1984). A localized cutting and herbiciding of *R. frangula* around the low-shrub zone may retard the closing in of this area. However, these benefits may only be short-lived because seedlings of *R. frangula* are common on sphagnum hummocks throughout the bog. Glossy buckthorn seedlings, however, were less common in the low-shrub zone at the time of this study.

Fire is effective in killing seedlings and small individuals of *Rhamnus frangula* (Heidorn, 1988; unpubl. report to the Illinois Nature Preserves Commission) but may not be sufficient to kill seedlings in saturated sphagnum hummocks. Without fire, seedlings of *R. frangula* would probably quickly join the tall-shrub stratum. *Rhamnus frangula* seedlings are too numerous at Gavin

Bog to control with herbicides without jeopardizing populations of threatened and endangered species. Although fire modifies and/or retards some community development in Michigan bogs, it usually does not prevent the expression of bog communities where conditions are suitable for their development (Gates, 1942).

In Michigan, recolonization patterns in severely burned bogs included a primary state dominated by *Epilobium angustifolium* L., with occasional *Conyza canadensis* (L.) Cronq. and *Rumex acetosella* L. Subsequent stages included *Rubus* species, while aspen often colonized these sites following a bramble association (Gates, 1942). On the other hand, presumably following a less severe fire where fire-sensitive tamaracks were not eliminated, the *Chamaedaphne* association regenerated itself and tamarack colonization occurred on any open site (Gates, 1942). In Wisconsin, bogs that have been burned have developed into a bog/sedge meadow hybrid community type (Curtis, 1959). No data are available on the vegetational response to fire in Illinois bogs. Experimental prescribed fires in Illinois bogs should be avoided when water levels are low, because the peat could be damaged or destroyed.

The long-term persistence of many of the rare floristic elements in Gavin Bog is dependent on a form of management that reduces the density of *Rhamnus frangula.* The shade-intolerant tamarack, for instance, is dependent on open areas for seedling establishment (Gates, 1942). *Vaccinium oxycoccos, V. myrtilloides, V. corymbosum, Betula pumila, Eriophorum virginicum, Ribes hirtellum,* and possibly *Sarracenia purpurea,* if still present in a suppressed vegetative condition or in the seed bank, may also benefit from management efforts that open up portions of the bog, either through cutting and stump treatment and/or fire. If portions of the bog were left unburned, the shade-tolerant species *Carex trisperma, C. brunnescens,* and *Trientalis borealis* would probably recolonize burned sites if a fire were to eliminate populations of these species. It is unlikely, however, that any known management practice will completely replace *R. frangula* with native species.

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## APPENDIX

Vascular flora of wetland and prairie communities at Gavin Bog Nature Preserve, Lake County, Illinois. A = alien, E = State endangered, S = State record (endangered), T = State threatened; bo = bog, ma = marsh, of = old field, pr = prairie, sm = sedge meadow; a = abundant, c = common, o = occasional, u = uncommon, r = rare.

**Equisetacea**

*Equisetum arvense* L.—ma, pr; c
*Equisetum fluviatile* L. var. *unilaterale* (Vasey) Malte—ma, sm; c
*Equisetum hyemale* L.—ma; o
*Equisetum laevigatum* A. Br.—pr; r
*Equisetum* × *ferrissii* Clute—ma; r

**Osmundaceae**

*Osmunda regalis* L.—bo; o
*Osmunda cinnamomea* L.—bo; c

**Thelypteridaceae**

*Thelypteris palustris* Schott—bo, sm; c

**Aspleniaceae**

*Onoclea sensibilis* L.—bo; o
*Dryopteris carthusiana* (Villars) H. P. Fuchs—bo; c

**Pinaceae**

*Larix laricina* (DuRoi) K. Koch T—bo; c

**Typhaceae**

*Typha latifolia* L.—ma; a

**Sparganiaceae**

*Sparganium androcladum* (Engelm.) Morong—ma; u
*Sparganium eurycarpum* Engelm.—sm, ma; o

**Alismaceae**

*Sagittaria latifolia* Willd.—bo, ma; c
*Alisma plantago-aquatica* L.—ma, bo; o

**Poaceae**

*Bromus kalmii* Gray—pr; r
*Poa pratensis* L. A—pr; o
*Poa compressa* L. A—pr, sm; o
*Poa trivialis* A—pr; r
*Sphenopholis obtusata* (Michx.) Scribn.—pr; u
*Calamagrostis canadensis* (Michx.) Beauv.—ma, sm, pr; a
*Agrostis alba* L. A—sm, pr, bo; o
*Phalaris arundinacea* L.—bo, ma, sm; c
*Phleum pratense* L. A—pr; r
*Elymus canadensis* L.—pr; o
*Agropyron trachycaulum* (Link) Malte var. *unilaterale* (Vasey) Malte E—pr; r

*Glyceria septentrionalis* Hitchc.—bo, ma, sm; c
*Glyceria striata* (Lam.) Hitchc.—pr, sm; o
*Dichanthelium acuminatum* (Sw.) Gould & Clark var. *fasciculatum* (Torr.) Freckm.—pr; r
*Dichanthelium acuminatum* (Sw.) Gould & Clark var. *lindheimeri* (Nash) Gould & Clark—pr; o
*Sorghastrum nutans* (L.) Nash—pr; c
*Andropogon gerardii* Vitm.—pr; c
*Schizachyrium scoparium* (Michx.) Nash—pr; o
*Spartina pectinata* Link—pr, sm; a
*Leersia oryzoides* (L.) Sw.—bo, ma; c

**Cyperaceae**

*Dulichium arundinaceum* (L.) Britt.—bo; o
*Eleocharis* cf. *macrostachya* Britt.—pr; o
*Eleocharis erythropoda* Steud.—ma; c
*Eleocharis obtusa* (Willd.) Schult.—ma; c
*Eleocharis elliptica* Kunth. var. *compressa* (Sull.) Drap. & Mohlenbr.—pr; o
*Scirpus acutus* Muhl.—ma, sm; c
*Scirpus heterochaetus* Chase—sm; o
*Scirpus fluviatilis* (Torr.) Gray—ma, sm; c
*Scirpus atrovirens* Willd.—ma; o
*Scirpus pendulus* Muhl.—pr; o
*Scirpus cyperinus* (L.) Kunth—ma, bo; o
*Eriophorum virginicum* L. E—bo; o
*Carex brunnescens* (Pers.) Poir. var. *sphaerostachya* (Tuckerm.) Kukenth. S—bo; c
*Carex sartwellii* Dew.—pr, sm; c
*Carex vulpinoidea* Michx.—ma, pr, sm; o
*Carex stipata* Muhl.—ma; o
*Carex trisperma* Dew. E—bo; o
*Carex interior* Bailey—pr; o
*Carex scoparia* Schk.—ma; c
*Carex tribuloides* Wahlenb.—pr, sm, bo; o
*Carex bebbii* Olney—bo, ma, pr; o
*Carex normalis* Mackenzie—pr, ma, sm; o
*Carex tenera* Dew.—pr; u
*Carex festucacea* Schk.—sm; c
*Carex stricta* Lam.—pr, sm; a
*Carex buxbaumii* Wahlenb.—ma, pr, sm; c
*Carex lasiocarpa* Ehrh.—pr; o
*Carex lanuginosa* Michx.—ma, pr, sm; o
*Carex granularis* Muhl.—pr; o
*Carex tetanica* Schk.—pr; o
*Carex lacustris* Willd.—ma, sm; o
*Carex atherodes* Spreng.—sm; o
*Carex comosa* Boott—ma; r
*Carex lupulina* Muhl.—bo; o

**Araceae**

*Acorus americanus* (Raf.) Raf.—ma; o

**Lemnaceae**

*Spirodela polyrhiza* (L.) Schleid.—ma; o
*Lemna minor* L.—ma; c

**Juncaceae**

*Juncus dudleyi* Wieg.—pr; o

**Liliaceae**

*Allium cernuum* Roth—pr; o
*Trillium recurvatum* Beck—pr; r
*Lilium michiganense* Farw.—pr; r
*Smilacina stellata* (L.) Desf.—pr; c
*Hypoxis hirsuta* (L.) Cov.—pr; o

**Iridaceae**

*Iris shrevei* Small—bo, ma, pr, sm; c
*Sisyrinchium albidum* Raf.—pr; o

**Orchidaceae**
*Cypripedium parviflorum* Salisb. E—pr; o
*Cypripedium* × *andrewsii* A. M. Fuller—pr; r
*Cypripedium candidum* Muhl. E—pr; o

**Salicaceae**
*Salix amygdaloides* Anderss.—ma, sm; r
*Salix alba* L. A—sm; r
*Salix rigida* Muhl.—pr, sm; u
*Salix glaucophylloides* Fern.—sm; o
*Salix bebbiana* Sarg.—sm, pr; o
*Salix discolor* Muhl.—pr, sm; o
*Salix humilis* Marsh.—pr; o
*Salix petiolaris* Sm.—ma, pr, sm; o
*Populus tremuloides* Michx.—pr; o

**Betulaceae**
*Betula papyrifera* Marsh.—bo; r
*Betula pumila* L.—bo; r

**Corylaceae**
*Corylus americana* Walt.—pr; r

**Fagaceae**
*Quercus alba* L.—bo; o
*Quercus macrocarpa* Michx.—pr; r

**Urticaceae**
*Boehmeria cylindrica* (L.) Sw.—ma; o

**Santalaceae**
*Comandra umbellata* (L.) Nutt.—pr; c

**Polygonaceae**
*Rumex crispus* L. A—pr; r
*Rumex orbiculatus* Gray—bo, ma; o
*Polygonum amphibium* L.—ma, sm; c

**Caryophyllaceae**
*Cerastium vulgatum* L. A—bo; r

**Ranunculaceae**
*Ranunculus sceleratus* L.—bo; r
*Ranunculus flabellaris* Raf.—ma, sm; c
*Thalictrum dasycarpum* Fisch. & Lall.—pr, sm; o
*Anemone virginiana* L.—pr, sm; o

**Berberidaceae**
*Podophyllum peltatum* L.—pr; c

**Brassicaceae**
*Cardamine bulbosa* (Schreb.) BSP.—ma, pr; o
*Cardamine pensylvanica* Muhl.—pr; r
*Rorippa islandica* (Oeder) Borbas var. *fernaldiana* Butt. & Abbe—ma; o
*Barbarea vulgaris* R. Br. A—pr; r

**Grossulariaceae**
*Ribes hirtellum* Michx. E—bo; r
*Ribes americanum* Mill.—bo, ma, pr; o

**Saxifragaceae**
*Penthorum sedoides* L.—bo; r
*Saxifraga pensylvanica* L.—pr; o
*Heuchera richardsonii* R. Br.—pr; o

**Rosaceae**
*Spiraea alba* DuRoi—ma, pr, sm; o
*Crataegus succulenta* Schrad.—pr; r
*Aronia melanocarpa* (Michx.) Ell.—bo; c
*Rubus occidentalis* L.—bo; r
*Rosa multiflora* Thunb. A—bo, sm; r
*Rosa carolina* L.—pr; o
*Rosa palustris* Marsh.—pr; o
*Fragaria virginiana* Duchesne—pr; c
*Geum canadense* Jacq.—pr; r
*Potentilla palustris* (L.) Scop.—ma; r

**Fabaceae**
*Lathyrus palustris* L.—pr, sm; o
*Apios americana* Medic.—pr; o

*Melilotus alba* Desr. N—pr; r
*Desmodium canadense* (L.) DC.—pr; o
*Amphicarpa bracteata* (L.) Fern.—pr; o
*Strophostyles leiosperma* (T. & G.) Piper—pr; o

**Oxalidaceae**
*Oxalis stricta* L.—pr; r

**Geraniaceae**
*Geranium maculatum* L.—pr; o

**Polygalaceae**
*Polygala senega* L.—pr; r

**Euphorbiaceae**
*Euphorbia corollata* L.—pr; r

**Aquifoliaceae**
*Ilex verticillata* (L.) Gray—bo, ma; c

**Aceraceae**
*Acer saccharinum* L.—bo, pr; r

**Balsaminaceae**
*Impatiens* cf. *capensis* Meerb.—bo; o

**Rhamnaceae**
*Rhamnus cathartica* L.—ma, pr; o
*Rhamnus frangula* L.—bo, ma, pr, sm; o-a

**Vitaceae**
*Parthenocissus quinquefolia* (L.) Planch.—sm; o
*Vitis riparia* Michx.—sm; o

**Hypericaceae**
*Triadenum fraseri* (Spach) Gl.—bo, pr; r

**Violaceae**
*Viola pratincola* Greene—pr, sm; c
*Viola* × *bernardii* Greene—pr, r
*Viola pedatifida* G. Don—pr; r
*Viola mackloskeyi* Lloyd spp. *pallens* (Banks) M. S. Baker—bo; r

**Lythraceae**
*Lythrum alatum* Pursh—bo, ma, pr, sm; o
*Lythrum salicaria* L. A—bo, ma, sm; o-a

**Onagraceae**
*Epilobium ciliatum* Raf.—bo; o
*Oenothera perennis* L. E—of; r

**Apiaceae**
*Eryngium yuccifolium* Michx.—pr; o
*Sanicula gregaria* Bickn.—pr; r
*Sanicula canadensis* L.—pr; r
*Oxypolis rigidior* (L.) Coult. & Rose—ma; o
*Zizia aurea* (L.) W. D. J. Koch—pr; c
*Sium suave* Walt.—bo, ma; a
*Cicuta maculata* L.—pr, sm; o

**Cornaceae**
*Cornus stolonifera* Michx.—bo, pr, sm; c
*Cornus obliqua* Raf.—bo, ma; o
*Cornus racemosa* Lam.—bo; o

**Pyrolaceae**
*Monotropa uniflora* L.—bo; r

**Ericaceae**
*Chamaedaphne calyculata* (L.) Moench T—bo; c
*Gaylussacia baccata* (Wang.) K. Koch—bo; o
*Vaccinium myrtilloides* Michx.—bo; u
*Vaccinium corymbosum* L. E—bo; o
*Vaccinium oxycoccos* L. S—bo; o

**Primulaceae**
*Dodecatheon meadia* L.—pr; o
*Lysimachia thyrsiflora* L.—bo, ma; o
*Lysimachia quadrifolia* L.—sm; o
*Trientalis borealis* Raf. T—bo; o

**Oleaceae**
*Fraxinus nigra* Marsh.—bo, pr; r

*Fraxinus pennsylvanica* Marsh.—bo; r

**Gentianaceae**

*Gentiana andrewsii* Griseb.—pr; r

**Apocynaceae**

*Apocynum sibiricum* Jacq.—pr, sm; o

**Asclepiadaceae**

*Asclepias incarnata* L.—ma, sm; c

**Convolvulaceae**

*Calystegia sepium* (L.) R. Br.—pr; r

**Cuscutaceae**

*Cuscuta* cf. *coryli* Engelm.—ma; r

**Polemoniaceae**

*Phlox pilosa* L.—pr; c

**Boraginaceae**

*Lithospermum canescens* (Michx.) Lehm.—pr; r

**Verbenaceae**

*Verbena hastata* L.—sm; o

**Lamiaceae**

*Mentha arvensis* L. var. *villosa* (Benth.) S. R. Stewart—bo, ma, sm; c

*Lycopus americanus* Muhl.—ma; o-c

*Lycopus uniflorus* Michx.—ma; c

*Teucrium canadense* L.—sm; o

*Scutellaria galericulata* L.—ma, sm; c

*Scutellaria lateriflora* L.—bo; o

*Monarda fistulosa* L.—pr; r

*Pycnanthemum virginianum* (L.) Dur. & Jacks.—sm; c

*Glechoma hederacea* L. A—bo; r

*Stachys palustris* L.—pr; o

*Prunella vulgaris* L.—pr; o

**Solanaceae**

*Solanum dulcamara* L. A—bo, ma; a

**Scrophulariaceae**

*Veronicastrum virginicum* (L.) Farw.—pr, sm; c

*Veronica scutellata* L. T—ma; o

*Pedicularis lanceolata* Michx.—pr; o

*Mimulus ringens* L.—pr, sm; o

*Castilleja coccinea* (L.) Spreng.—pr; o

**Lentibulariaceae**

*Utricularia vulgaris* L.—ma; c

**Acanthaceae**

*Ruellia humilis* Nutt.—pr; o

**Plantaginaceae**

*Plantago major* L. A—pr; r

**Rubiaceae**

*Galium boreale* L.—bo, pr, sm; c

*Galium obtusum* Bigel.—bo, pr; o

*Galium tinctorium* L.—ma; o

*Galium triflorum* Michx.—pr; o

**Caprifoliaceae**

*Sambucus canadensis* L.—bo, sm; r

*Lonicera morrowi* Gray A—bo; r

*Viburnum opulus* L. A—pr; r

*Viburnum lentago* L.—pr, bo; r

*Viburnum recognitum* Fern.—bo; u

**Campanulaceae**

*Campanula aparinoides* Pursh—ma, sm; o

*Lobelia spicata* Lam.—pr; o

**Asteraceae**

*Ambrosia artemisiifolia* L.—pr; r

*Aster ericoides* L.—pr; c

*Aster novae-angliae* L.—pr, sm; c

*Aster pilosus* Willd.—pr; o

*Aster praealtus* Poir.—pr; o

*Aster puniceus* L.—ma, sm; o

*Aster simplex* Willd.—pr; o

*Erigeron philadelphicus* L.—pr; r

*Erigeron strigosus* Muhl.—pr; o

*Bidens cernua* L.—ma; o

*Bidens tripartita* L.—ma; o

*Cirsium* sp.—pr; r

*Eupatorium maculatum* L.—ma, pr, sm; o
*Eupatorium perfoliatum* L.—ma, sm; o
*Helenium autumnale* L.—pr; o
*Helianthus grosseserratus* Martens—pr, sm; c
*Helianthus rigidus* (Cass.) Desf.—pr; o
*Krigia biflora* (Walt.) Blake—pr; o
*Liatris pycnostachya* Michx.—pr; c
*Liatris spicata* (L.) Willd.—pr; o
*Ratibida pinnata* (Vent.) Barnh.—pr; o
*Rudbeckia hirta* L.—pr; o
*Rudbeckia subtomentosa* Pursh—pr; o-c
*Rudbeckia triloba* L.—sm, pr; u
*Senecio aureus* L.—pr; c
*Silphium integrifolium* Michx.—pr; o
*Silphium laciniatum* L.—pr; c
*Silphium terebinthinaceum* Jacq.—pr; a
*Solidago gigantea* Ait.—sm; o
*Solidago riddellii* Frank—pr; o
*Solidago rigida* L.—pr; o
*Euthamia graminifolia* (L.) Salisb.—sm; o
*Taraxacum officinale* Weber—pr; r
*Vernonia fasciculata* Michx.—pr; o

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# THE MARSH VEGETATION OF THREE CONNECTICUT RIVER OXBOWS: A TEN-YEAR COMPARISON

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## ABSTRACT

The floras and vegetation of marshes in three large Connecticut River oxbows of differing ages in western Massachusetts were studied and compared in 1974 and again in 1984. Marshes at Hatfield in the most recently formed of the three oxbows occur in zones that parallel much of the old river bank. Marshes in Ned's Ditch, Northampton, an oxbow segment that was cut off from the river around 710 yr. B.P., occur within nine scattered ponds surrounded by swamp forest. Marshes at Whately in the oldest oxbow are confined to the vicinity of a single pond. In all three oxbows, a high marsh is dominated by *Onoclea sensibilis* and a low marsh by *Lemna minor* and *Nuphar variegatum*. Zones of emergent mid marsh vegetation are distinctive at each oxbow. Marshes at the two younger, regularly flooded oxbows share numerous species with the herb strata of adjacent swamp forests and remained relatively unchanged throughout the study period except for an increase in woody seedlings at the Hatfield high marsh. The Whately marshes share few species with adjacent forest; species richness in high and emergent zones of the Whately marshes declined sharply over the decade.

Key Words: marsh vegetation, wetlands, floodplains, Connecticut River, Massachusetts

## INTRODUCTION

Marshes and other floodplain habitats along major streams in New England are spatiallly restricted and frequently disturbed by human activities. In western Massachusetts, extensive marsh vegetation occurs in four large oxbow lakes located along an 18 km stretch of the Connecticut River. A study of the vegetation of these marshes was included within broader studies of the phytosociology and geological development of the three older oxbows by M. M. Holland (Sackett, 1974, Unpubl. Master's thesis, Smith College, Northampton, Mass.; 1977, Unpubl. Ph.D. dissertation, U. Mass., Amherst). Field research for these earlier studies was conducted during the period 1973–1975. More recently, the relative ages of these oxbows have been established (Holland and Burk, 1982) and the herbaceous strata of swamp forests in the three older oxbows compared (Holland and Burk, 1984).

Within the context of an ongoing long-term study, observations of the Whately oxbow in the late 1970's and early 1980's indicated

that marked changes in the vegetation had occurred some time after 1975. In addition, continuing investigations in the southeastern section of the prehistoric oxbow in Northampton, a large marsh complex which includes segments known as Hulbert's Pond and the Wood Duck Pond, have shown that the structure and composition of marsh vegetation were strongly influenced through the period 1969–1980 by changes in water quality in both the Connecticut River and in the Mill River, a tributary of the Connecticut that has preempted a portion of the oxbow (Robinton and Burk, 1971; Burk, 1973, 1977; Burk and Holland, 1981). Damage to vegetation caused by an oil spill in Hulbert's Pond and the Wood Duck Pond and changes through the recovery period (Burk, 1977) were also found to be similar to long-term marsh destruction in a Massachusetts salt marsh (Hampson and Moul, 1977, 1978).

Oxbows have classically been considered to support communities that are transitional between open water and adjacent terrestrial habitats. Clements and Shelford (1939) observed, for example, "that any portion of a community separated from the river channel, such as an oxbow, takes an immediate start as a land sere, characterized by increases in vegetation and the extinction of the terrigenous bottom community." Oxbows of differing ages in a given area can be considered as a chronosequence, a "spatial array" of sites that can be arranged in a pattern representing successional development from the initial stages available for colonization to the climax community of the region (Barbour et al., 1987; Jackson et al., 1988). Recent work, however, suggests that disturbance resulting from human activities may significantly influence the vegetation of apparent chronosequences and short-term effects of disturbance can be erroneously confused with long-term developmental trends (Jackson et al., 1988).

The major purpose of the present study was to examine the marshes of the three older oxbows and to compare the dominance (contribution to cover) and distribution of the vascular plant species present in 1974 with their dominance and distribution a decade later. Because of the changes documented at Hulbert's Pond and observed at the Whately oxbow, particular attention was paid to possible deterioration of the marsh environments, including changes in the status of non-native species that might be potential indicators of disturbance. Shelford (1963) estimated that convergence to forest vegetation in oxbows and other long

submergence habitats would require "not less than 1,000 years" for completion in the Mississippi floodplain, and we did not expect to observe major successional changes over the course of the decade in New England, where vegetational processes proceed at a slower rate. However, Larson and Golet (1982), in an analysis of wetland habitats on the Massachusetts coastal plain, demonstrated that, while deep open water and forested wetland habitats are relatively stable, marshes frequently undergo transitions to shrub swamp or forested wetlands within a period of less than twenty years. Hence, the data were also examined for any indications that successional change might be occurring, including the relative degrees of overlap between the floras of the marshes and those of adjacent oxbow swamp forest habitats. The status of uncommon or rare native plants was also noted, since oxbow habitats often support relics of formerly more widespread floras and vegetation types (Holland and Burk, 1984).

## THE STUDY SITES

Maps of the four oxbows and the locations of the study sites are included in Holland and Burk (1982, 1984). The 1840 Northampton oxbow remains predominantly open water with direct connections to the Connecticut River. Because this oxbow is used extensively for boating, water-skiing, and other recreational activities, its vegetation has been excluded from this investigation.

**The Hatfield oxbow.** The Hatfield oxbow, youngest (i.e., most recently separated from the main stem of the Connecticut) of the three sites that were studied, was depicted as two large ponds in early maps of the area. In March, 1936, during heavy flooding, the Connecticut River flowed directly through the Hatfield oxbow, causing extensive scouring of the bottom sediments (Collins and Schalk, 1937). Marshes are extensive in the Hatfield oxbow, occupying roughly two thirds of the old river bed as determined by aerial photographs, USGS topographic maps, local maps available from various sources, and ground and aerial reconnaissance. The oxbow is flooded from the Connecticut at least yearly, and in late May, 1984, was inundated for more than a week. The oxbow also receives more or less continuous flow from a small tributary known as Cow Bridge Brook.

**Ned's Ditch.** This prehistoric Northampton oxbow was separated from the Connecticut River around 710 (±130) yr. B.P. as

determined by stratigraphy and radiocarbon dating (Holland and Burk, 1982). The southeastern portion of the oxbow contains the Hulbert's Pond marsh complex. Much of the remainder of the oxbow is included in a segment known as Ned's Ditch. Ned's Ditch is largely forested but contains an estimated 16 ha of marsh vegetation associated with seven ponds and two remnants of an earlier, abandoned bed of the Mill River. During periods of high water on the Connecticut, much of Ned's Ditch, including the forest, is flooded. The southeastern section of the prehistoric Northampton oxbow was excluded from this study because of the extensive work already conducted there (Robinton and Burk, 1971; Burk, 1973, 1977; Burk and Holland, 1981).

**The Whately oxbow.** The Whately oxbow is the oldest and most heavily forested of the four sites, lying largely above the present floodplain of the Connecticut. An estimated 8 ha of marsh vegetation occurs in the lower portions of the Whately site, surrounding and extending south of the remaining open water, a small pond fed and drained by a brook in the southeast corner of the oxbow. The area including the marsh was flooded in 1936, possibly for the first time since being raised above the active floodplain "many hundreds, perhaps even a few thousand years ago" (Jahns, 1947).

Full descriptions of the study sites are reported in Holland and Burk (1982, 1984).

## MARSH HABITATS AND SAMPLING METHODS

The marsh habitats of the three oxbows exhibit a developmental topographic sequence from (1) more or less continuous vegetation along the edges of the old riverbed at Hatfield to (2) scattered ponds, each surrounded by marsh, at Ned's Ditch, to (3) a single remnant pond with associated marshes at Whately. At all three sites, wherever marsh vegetation occurs, three discrete zones of vegetation usually can be identified without difficulty in sequence from the river bank towards open water. These areas are comparable to the zones described by Daubenmire (1968) and other authors as stages in lake and pond succession, and are characterized by vascular plant species with life forms adapted to particular water depths. High marsh, forming a mat closest to the river bank, has herbaceous vegetation growing in constantly wet soil with no standing water under normal conditions during the

time of year when vegetation is most fully developed. Mid marsh is characterized by emergent, anchored hydrophytes; standing water is usually present between plant stems. Low marsh is characterized by hydrophytes that are submerged, floating, or rooted with floating leaves. The submerged and floating forms may be either anchored or free-moving in the water [i.e., the "errant vascular hydrophytes" of Mueller-Dombois and Ellenberg (1974)].

Sampling techniques varied somewhat with site conditions.

**Hatfield.** At Hatfield in 1974, ten belt transects approximately 300 m long and 1 m wide were established across the oxbow at intervals of 575 m, as part of a general survey of vegetation types (Holland and Burk, 1984; Sackett, 1977 op. cit.). Marsh vegetation occurred on eight transects and was accessible on six. On each transect sampled, ten 0.5 m × 0.5 m quadrats were evenly spaced in each zone at intervals of 1 m on a baseline perpendicular to the transect. The baselines were situated to avoid transitional areas between zones; quadrats that were overlaid by flood debris were relocated to the nearest undisturbed vegetation on the baseline. In each quadrat, a visual estimate of percentage cover was determined and recorded for each vascular plant species present. On some transects, one of the three typical zones was absent. On other transects, one or more zones of marsh occurred at two discrete and separate intervals along the transect and were included twice in sampling. In all, eight areas of high marsh, six areas of mid marsh, and six areas of low march were sampled.

**Ned's Ditch.** In 1974, a line transect was run from south to north across each of the seven ponds and two sections of the old Mill River bed. All nine marsh units are hereafter referred to as ponds; maps of Ned's Ditch with locations of the ponds are in Sackett (1974, op. cit.). Usually the transect crossed the sequence high marsh/mid marsh/low marsh/mid marsh/high marsh. In each pond, 0.5 m × 0.5 m quadrats were placed and sampled as at Hatfield in the southernmost zone of high and mid marsh and in the center of low marsh. Occasionally one zone was lacking. Five areas of high marsh, seven of mid marsh, and nine of low marsh were sampled in 1974.

**Whately.** Marsh vegetation was sampled as at Hatfield on two transects, one crossing the pond and the other crossing its drainage. Two areas of high marsh, two of mid marsh, and two of low marsh were sampled in 1974.

In 1984, all transects with marsh vegetation were relocated and

vegetation sampled as before. In Ned's Ditch, four new zones had become established and seven zones of high marsh, nine of mid marsh, and nine of low marsh could be studied. The sampling procedure, which was regular and non-random, assured that the same zones on the same transects across the oxbow were studied in both 1974 and 1984. The baselines on which the quadrats were situated were not necessarily the same, however, particularly in instances where the position of the zones along the transects may have shifted.

For analysis and comparison, Table 1 was prepared to document the floras of the marshes in 1974 and 1984 as determined by quantitative sampling. Average percent cover and frequency of each species sampled in each of the three zones in each oxbow during 1974 and 1984 are listed with cover values and frequencies rounded off to the nearest whole number. Table 1 also includes summed cover values for each zone, computed on the basis of actual rather than rounded data, and species richness, the total number of species present in each zone. Cover data are particularly useful because they allow comparisons of the amount of surface occupied by plants of differing life forms (Daubenmire, 1968). Frequency, expressed as percent occurrence in a given number of sample plots, serves as a measurement of the distribution of the species throughout the zone. The relative importance of cover and frequency in assessing changes in vegetation depends to a large extent on the life forms of the plants involved. Tree seedlings may occur, for example, with low cover but high frequency in a zone, and their frequency might be interpreted as an indication of successful reproduction and potential change (Mueller-Dombois and Ellenberg, 1974). In contrast, low cover and high frequency of errant hydrophytes such as *Lemna minor* L. in the upper marsh zones or swamp forest of the oxbows may simply reflect the persistence of the plants after being stranded after periods of high water (Holland and Burk, 1984).

Because the placement of the quadrats in this study was not random, probability statistics are inappropriate as aids in interpreting whether significant vegetational change has occurred (Mueller-Dombois and Ellenberg, 1974; Barbour et al., 1987). However, the data do lend themselves to comparisons through indices of similiarity. We have used the Simpson Index of Resemblance (Simpson, 1965) to compare the taxonomic composition of the floras of the marshes (Table 2), combining data from

Table 1. Percent cover (**C**), frequency (**F**), zone(s), and year(s) of occurrence of species sampled in each zone of the three oxbow marshes in 1974 and 1984. **H** indicates high marsh; **M** indicates mid marsh; **L** indicates low marsh. Total cover is the sum of actual cover values for each species.

| | | Hatfield | | | | Ned's Ditch | |
|---|---|---|---|---|---|---|---|
| | | 1974 | | 1984 | | 1974 | |
| Species | Zone | C | F | C | F | C | F |
| Herbs and vines | | | | | | | |
| *Actaea rubra* (Ait.) Willd. | H | – | – | <.5 | 1 | – | – |
| *Agrostis alba* L. | H | – | – | – | – | 1 | 10 |
| | M | – | – | – | – | – | |
| | L | – | – | – | – | <.5 | 2 |
| *Alisma subcordatum* Raf. | H | – | – | – | – | <.5 | 4 |
| | M | – | – | – | – | – | – |
| *Amphicarpa bracteata* (L.) Fern. | H | – | – | <.5 | 1 | – | – |
| *Apios americana* Medic. | H | 3 | 25 | 2 | 16 | 1 | 6 |
| *Arisaema triphyllum* (L.) Schott | H | – | – | <.5 | 3 | <.5 | 2 |
| *Athyrium filix-femina* (L.) Roth | H | – | – | – | – | – | – |
| *Bidens tripartita* L. | H | <.5 | 8 | 1 | 19 | <.5 | 2 |
| | M | 1 | 5 | <.5 | 10 | – | – |
| *Boehmeria cylindrica* (L.) Sw. | H | 1 | 28 | 2 | 23 | <.5 | 6 |
| | M | <.5 | 3 | <.5 | 9 | – | – |
| | L | <.5 | 5 | – | – | – | – |
| *Cabomba caroliniana* Gray | M | 1 | 30 | 2 | 13 | – | – |
| | L | 3 | 13 | 4 | 15 | – | – |
| *Calamagrostis canadensis* (Michx.) Nutt. | H | <.5 | 6 | – | – | – | – |
| | M | <.5 | 2 | – | – | – | – |

Table 1. Continued.

| Species | Zone | Ned's Ditch 1984 C | Ned's Ditch 1984 F | Whately 1974 C | Whately 1974 F | Whately 1984 C | Whately 1984 F |
|---|---|---|---|---|---|---|---|
| Herbs and vines | | | | | | | |
| *Actaea rubra* (Ait.) Willd. | H | – | – | – | – | – | – |
| *Agrostis alba* L. | H | – | – | 6 | 40 | – | – |
| | M | – | – | 4 | 30 | – | – |
| | L | – | – | – | – | – | – |
| *Alisma subcordatum* Raf. | H | – | – | – | – | – | – |
| | M | – | – | <.5 | 5 | – | – |
| *Amphicarpa bracteata* (L.) Fern. | H | – | – | – | – | – | – |
| *Apios americana* Medic. | H | 5 | 26 | – | – | 1 | 10 |
| *Arisaema triphyllum* (L.) Schott | H | – | – | – | – | – | – |
| *Athyrium filix-femina* (L.) Roth | H | – | – | 2 | 20 | – | – |
| *Bidens tripartita* L. | H | 3 | 47 | – | – | <.5 | 5 |
| | M | 4 | 49 | <.5 | 10 | – | – |
| *Boehmeria cylindrica* (L.) Sw. | H | <.5 | 1 | 2 | 30 | <.5 | 15 |
| | M | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Cabomba caroliniana* Gray | M | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Calamagrostis canadensis* (Michx.) Nutt. | H | – | – | – | – | – | – |
| | M | – | – | – | – | – | – |

Table 1. Continued.

| Species | Zone | Hatfield 1974 C | Hatfield 1974 F | Hatfield 1984 C | Hatfield 1984 F | Ned's Ditch 1974 C | Ned's Ditch 1974 F |
|---|---|---|---|---|---|---|---|
| *Callitriche heterophylla* Pursh | H | <.5 | 9 | <.5 | 4 | – | – |
| | L | 1 | 13 | – | – | – | – |
| *Cardamine pensylvanica* Muhl. | H | <.5 | 1 | – | – | – | – |
| | M | – | – | – | – | – | – |
| *Carex* spp.[1] | H | 1 | 15 | 2 | 28 | – | – |
| | M | <.5 | 7 | 1 | 15 | – | – |
| | L | – | – | <.5 | 3 | – | – |
| *Ceratophyllum demersum* L. | M | <.5 | 17 | 2 | 13 | – | – |
| | L | 3 | 17 | 2 | 12 | – | – |
| *Cicuta maculata* L. | H | – | – | – | – | – | – |
| | M | – | – | – | – | – | – |
| | L | <.5 | 2 | – | – | – | – |
| *Convolvulus sepium* L. | H | <.5 | 3 | – | – | – | – |
| *Cuscuta gronovii* Willd. | H | <.5 | 1 | – | – | – | – |
| | M | <.5 | 13 | <.5 | 5 | – | – |
| | L | <.5 | 2 | – | – | – | – |
| *Dryopteris spinulosa* (O. F. Muell.) Watt | H | <.5 | 1 | – | – | 3 | 22 |
| | M | – | – | – | – | <.5 | 4 |
| *Dulichium arundinaceum* (L.) Britt. | H | – | – | 1 | 3 | – | – |
| | M | – | – | – | – | – | – |
| *Echinocystis lobata* (Michx.) T. & G. | H | <.5 | 3 | – | – | – | – |
| *Eleocharis acicularis* (L.) R. & S. | H | – | – | – | – | 4 | 12 |
| | M | – | – | – | – | <.5 | 3 |

Table 1. Continued.

| Species | Zone | Ned's Ditch 1984 C | Ned's Ditch 1984 F | Whately 1974 C | Whately 1974 F | Whately 1984 C | Whately 1984 F |
|---|---|---|---|---|---|---|---|
| *Callitriche heterophylla* Pursh | H | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Cardamine pensylvanica* Muhl. | H | – | – | – | – | <.5 | 5 |
| | M | – | – | <.5 | 5 | – | – |
| *Carex* spp.[1] | H | – | – | 9 | 50 | <.5 | 5 |
| | M | – | – | 3 | 15 | – | – |
| | L | – | – | – | – | – | – |
| *Ceratophyllum demersum* L. | M | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Cicuta maculata* L. | H | – | – | 3 | 35 | – | – |
| | M | – | – | <.5 | 15 | – | – |
| | L | – | – | – | – | – | – |
| *Convolvulus sepium* L. | H | – | – | – | – | – | – |
| *Cuscuta gronovii* Willd. | H | – | – | <.5 | 5 | – | – |
| | M | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Dryopteris spinulosa* (O. F. Muell.) Watt | H | – | – | – | – | – | – |
| | M | – | – | – | – | – | – |
| *Dulichium arundinaceum* (L.) Britt. | H | 1 | 11 | – | – | – | – |
| | M | <.5 | 2 | – | – | – | – |
| *Echinocystis lobata* (Michx.) T. & G. | H | – | – | – | – | – | – |
| *Eleocharis acicularis* (L.) R. & S. | H | 1 | 4 | – | – | – | – |
| | M | – | – | – | – | 3 | 20 |

Table 1. Continued.

| Species | Zone | Hatfield 1974 C | Hatfield 1974 F | Hatfield 1984 C | Hatfield 1984 F | Ned's Ditch 1974 C | Ned's Ditch 1974 F |
|---|---|---|---|---|---|---|---|
| *Eleocharis intermedia* (Muhl.) Schultes | H | – | – | – | – | – | – |
| | M | – | – | – | – | – | – |
| *Eleocharis obtusa* (Willd.) Schultes | H | <.5 | 1 | – | – | – | – |
| *Elodea nuttallii* (Planch.) St. John | M | 1 | 7 | <.5 | 1 | – | – |
| | L | 3 | 12 | – | – | – | – |
| *Equisetum fluviatile* L. | H | <.5 | 9 | 3 | 11 | – | – |
| | M | <.5 | 2 | 2 | 11 | – | – |
| | L | <.5 | 5 | <.5 | 3 | – | – |
| *Eupatorium maculatum* L. | H | – | – | <.5 | 1 | – | – |
| *Eupatorium perfoliatum* L. | H | – | – | – | – | – | – |
| *Galium aparine* L. | H | – | – | – | – | – | – |
| | M | – | – | – | – | – | – |
| *Galium trifidum* L. | H | <.5 | 18 | 1 | 41 | <.5 | 6 |
| | M | <.5 | 3 | <.5 | 5 | <.5 | 1 |
| | L | <.5 | 2 | – | – | – | – |
| *Geum canadense* Jacq. | H | – | – | – | – | – | – |
| *Glechoma hederacea* L. | H | – | – | – | – | – | – |
| *Glyceria canadensis* (Michx.) Trin. | H | – | – | – | – | – | – |
| | M | – | – | – | – | – | – |
| *Glyceria striata* (Lam.) Hitchc. | H | 1 | 6 | – | – | – | – |
| *Hypericum perforatum* L. | H | – | – | – | – | – | – |
| | M | – | – | – | – | – | – |

Table 1. Continued.

| Species | Zone | Ned's Ditch 1984 C | Ned's Ditch 1984 F | Whately 1974 C | Whately 1974 F | Whately 1984 C | Whately 1984 F |
|---|---|---|---|---|---|---|---|
| *Eleocharis intermedia* (Muhl.) Schultes | H | – | – | 1 | 15 | – | – |
| | M | – | – | 1 | 10 | – | – |
| *Eleocharis obtusa* (Willd.) Schultes | H | – | – | – | – | – | – |
| *Elodea nuttallii* (Planch.) St. John | M | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Equisetum fluviatile* L. | H | – | – | – | – | – | – |
| | M | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Eupatorium maculatum* L. | H | – | – | – | – | – | – |
| *Eupatorium perfoliatum* L. | H | – | – | 1 | 15 | – | – |
| *Galium aparine* L. | H | – | – | 4 | 45 | – | – |
| | M | – | – | 1 | 15 | – | – |
| *Galium trifidum* L. | H | <.5 | 6 | – | – | 1 | 5 |
| | M | – | – | – | – | 1 | 5 |
| | L | – | – | – | – | – | – |
| *Geum canadense* Jacq. | H | – | – | <.5 | 5 | – | – |
| *Glechoma hederacea* L. | H | – | – | <.5 | 5 | – | – |
| *Glyceria canadensis* (Michx.) Trin. | H | – | – | – | – | 1 | 5 |
| | M | – | – | – | – | 1 | 10 |
| *Glyceria striata* (Lam.) Hitchc. | H | – | – | – | – | – | – |
| *Hypericum perforatum* L. | H | – | – | <.5 | 10 | – | – |
| | M | – | – | 1 | 5 | – | – |

Table 1. Continued.

| Species | Zone | Hatfield 1974 C | Hatfield 1974 F | Hatfield 1984 C | Hatfield 1984 F | Ned's Ditch 1974 C | Ned's Ditch 1974 F |
|---|---|---|---|---|---|---|---|
| *Hypericum virginicum* L. | H | – | – | – | – | – | – |
| *Impatiens capensis* Meerb. | H | 1 | 13 | <.5 | 4 | – | – |
| | M | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Iris versicolor* L. | L | <.5 | 2 | – | – | – | – |
| *Juncus effusus* L. | H | – | – | – | – | – | – |
| | M | – | – | – | – | – | – |
| *Leersia oryzoides* (L.) Sw. | H | 1 | 14 | 2 | 40 | <.5 | 4 |
| | M | 14 | 17 | 3 | 13 | <.5 | 1 |
| | L | 2 | 17 | 1 | 10 | – | – |
| *Lemna minor* L. | H | 1 | 10 | <.5 | 25 | <.5 | 16 |
| | M | 57 | 93 | 18 | 75 | 2 | 71 |
| | L | 28 | 62 | 27 | 73 | 1 | 56 |
| *Lindernia dubia* (L.) Pennell | H | <.5 | 5 | <.5 | 3 | – | – |
| | M | <.5 | 2 | – | – | – | – |
| *Ludwigia palustris* (L.) Ell. | H | 1 | 6 | – | – | 4 | 10 |
| | M | 1 | 2 | – | – | – | – |
| *Ludwigia polycarpa* Short & Peter | H | – | – | – | – | <.5 | 4 |
| *Lycopus virginicus* L. | H | – | – | – | – | – | – |
| | M | <.5 | 2 | <.5 | 1 | – | – |
| *Lysimachia ciliata* L. | H | – | – | <.5 | 1 | – | – |
| *Lysimachia terrestris* (L.) B.S.P. | H | – | – | – | – | – | – |
| | M | – | – | – | – | – | – |

Table 1. Continued.

| Species | Zone | Ned's Ditch 1984 C | Ned's Ditch 1984 F | Whately 1974 C | Whately 1974 F | Whately 1984 C | Whately 1984 F |
|---|---|---|---|---|---|---|---|
| *Hypericum virginicum* L. | H | 1 | 8 | – | – | – | – |
| *Impatiens capensis* Meerb. | H | – | – | 8 | 55 | 9 | 45 |
| | M | – | – | 8 | 35 | 14 | 40 |
| | L | – | – | 2 | 10 | – | – |
| *Iris versicolor* L. | L | – | – | – | – | – | – |
| *Juncus effusus* L. | H | – | – | 7 | 30 | – | – |
| | M | – | – | <.5 | 5 | – | – |
| *Leersia oryzoides* (L.) Sw. | H | <.5 | 7 | 6 | 35 | 1 | 15 |
| | M | 2 | 19 | 17 | 45 | – | – |
| | L | <.5 | 3 | – | – | – | – |
| *Lemna minor* L. | H | <.5 | 6 | – | – | <.5 | 5 |
| | M | 1 | 74 | 12 | 60 | 5 | 50 |
| | L | 1 | 50 | 1 | 75 | 1 | 50 |
| *Lindernia dubia* (L.) Pennell | H | – | – | – | – | – | – |
| | M | – | – | – | – | – | – |
| *Ludwigia palustris* (L.) Ell. | H | – | – | <.5 | 5 | – | – |
| | M | – | – | <.5 | 10 | – | – |
| *Ludwigia polycarpa* Short & Peter | H | – | – | – | – | – | – |
| *Lycopus virginicus* L. | H | – | – | 2 | 25 | – | – |
| | M | – | – | – | – | – | – |
| *Lysimachia ciliata* L. | H | – | – | 1 | 10 | – | – |
| *Lysimachia terrestris* (L.) B.S.P. | H | 1 | 11 | 1 | 10 | – | – |
| | M | – | – | <.5 | 5 | – | – |

Table 1. Continued.

| Species | Zone | Hatfield 1974 C | Hatfield 1974 F | Hatfield 1984 C | Hatfield 1984 F | Ned's Ditch 1974 C | Ned's Ditch 1974 F |
|---|---|---|---|---|---|---|---|
| *Lysimachia nummularia* L. | H | – | – | – | – | <.5 | 4 |
| *Lythrum salicaria* L. | H | 1 | 3 | – | – | – | – |
| | M | 2 | 15 | – | – | – | – |
| *Maianthemum canadense* Desf. | H | <.5 | 1 | – | – | – | – |
| *Matteuccia struthiopteris* (L.) Tod. | H | 1 | 9 | – | – | <.5 | 2 |
| *Mimulus ringens* L. | M | – | – | <.5 | 3 | – | – |
| *Myosotis scorpiodes* L. | M | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Nuphar variegatum* Engelm. | M | – | – | 1 | 3 | 2 | 25 |
| | L | 7 | 17 | 11 | 25 | 7 | 53 |
| *Nymphaea odorata* Ait. | M | – | – | 1 | 4 | – | – |
| | L | – | – | 7 | 23 | – | – |
| *Onoclea sensibilis* L. | H | 50 | 93 | 43 | 93 | 15 | 44 |
| | M | – | – | 4 | 9 | – | – |
| | L | – | – | <.5 | 2 | – | – |
| *Osmunda regalis* L. | H | <.5 | 1 | 2 | 3 | 6 | 16 |
| | M | – | – | – | – | 2 | 4 |
| *Oxalis europaea* Jord. | H | <.5 | 6 | <.5 | 8 | – | – |
| *Panicum lanuginosum* Ell. | H | – | – | <.5 | 1 | – | – |
| *Panicum* sp. | H | – | – | – | – | – | – |
| *Parthenocissus quinquefolia* (L.) Planch. | H | <.5 | 14 | <.5 | 3 | – | – |
| | M | <.5 | 2 | – | – | – | – |

Table 1. Continued.

| Species | Zone | Ned's Ditch 1984 C | Ned's Ditch 1984 F | Whately 1974 C | Whately 1974 F | Whately 1984 C | Whately 1984 F |
|---|---|---|---|---|---|---|---|
| *Lysimachia nummularia* L. | H | <.5 | 1 | – | – | – | – |
| *Lythrum salicaria* L. | H | – | – | – | – | – | – |
| | M | – | – | – | – | – | – |
| *Maianthemum canadense* Desf. | H | – | – | – | – | – | – |
| *Matteuccia struthiopteris* (L.) Tod. | H | 1 | 6 | – | – | – | – |
| *Mimulus ringens* L. | M | – | – | – | – | – | – |
| *Myosotis scorpiodes* L. | M | – | – | – | – | <.5 | 5 |
| | L | – | – | – | – | 1 | 5 |
| *Nuphar variegatum* Engelm. | M | 7 | 17 | – | – | – | – |
| | L | 12 | 36 | 12 | 25 | 16 | 30 |
| *Nymphaea odorata* Ait. | M | – | – | – | – | – | – |
| | L | – | – | – | – | 11 | 30 |
| *Onoclea sensibilis* L. | H | 23 | 47 | 14 | 50 | 56 | 95 |
| | M | – | – | 2 | 10 | 8 | 25 |
| | L | – | – | – | – | – | – |
| *Osmunda regalis* L. | H | 20 | 40 | – | – | – | – |
| | M | – | – | – | – | – | – |
| *Oxalis europaea* Jord. | H | – | – | <.5 | 10 | – | – |
| *Panicum lanuginosum* Ell. | H | – | – | – | – | 4 | 25 |
| *Panicum* sp. | H | <.5 | 1 | – | – | – | – |
| *Parthenocissus quinquefolia* (L.) Planch. | H | – | – | – | – | <.5 | 5 |
| | M | – | – | – | – | – | – |

Table 1. Continued.

| Species | Zone | Hatfield 1974 C | Hatfield 1974 F | Hatfield 1984 C | Hatfield 1984 F | Ned's Ditch 1974 C | Ned's Ditch 1974 F |
|---|---|---|---|---|---|---|---|
| *Peltandra virginica* (L.) Schott & Endl. | H | – | – | <.5 | 8 | – | – |
| | M | 10 | 35 | 14 | 25 | – | – |
| *Pilea pumila* (L.) Gray | H | – | – | <.5 | 1 | – | – |
| | M | – | – | <.5 | 1 | – | – |
| *Poa palustris* L. | H | – | – | – | – | – | – |
| *Polygonum amphibium* L. | H | – | – | – | – | <.5 | 2 |
| *Polygonum arifolium* L. | H | – | – | – | – | – | – |
| *Polygonum hydropiperoides* Michx. | M | – | – | 1 | 7 | – | – |
| *Polygonum sagittatum* L. | H | <.5 | 1 | – | – | – | – |
| *Polygonum* spp. | L | – | – | 1 | 5 | – | – |
| *Pontederia cordata* L. | H | <.5 | 1 | – | – | – | – |
| *Potamogeton pectinatus* L. | M | – | – | – | – | 1 | 36 |
| | L | <.5 | 2 | – | – | 7 | 37 |
| *Ranunculus flabellaris* Raf. | H | – | – | – | – | <.5 | 10 |
| | M | – | – | – | – | <.5 | 7 |
| | L | – | – | – | – | <.5 | 1 |
| *Rhus radicans* L. | H | <.5 | 1 | <.5 | 1 | <.5 | 2 |
| *Rumex crispus* L. | M | – | – | – | – | – | – |
| *Sagittaria latifolia* Willd. | H | <.5 | 1 | <.5 | 1 | – | – |
| | M | <.5 | 2 | 1 | 8 | – | – |
| | L | – | – | <.5 | 2 | <.5 | 6 |
| *Scirpus atrovirens* Willd. | H | – | – | – | – | – | – |

Table 1. Continued.

| Species | Zone | Ned's Ditch 1984 C | Ned's Ditch 1984 F | Whately 1974 C | Whately 1974 F | Whately 1984 C | Whately 1984 F |
|---|---|---|---|---|---|---|---|
| *Peltandra virginica* (L.) Schott & Endl. | H | – | – | – | – | – | – |
| | M | – | – | – | – | – | – |
| *Pilea pumila* (L.) Gray | H | – | – | – | – | 1 | 10 |
| | M | – | – | – | – | – | – |
| *Poa palustris* L. | H | – | – | 5 | 30 | – | – |
| *Polygonum amphibium* L. | H | – | – | – | – | – | – |
| *Polygonum arifolium* L. | H | – | – | <.5 | 5 | – | – |
| *Polygonum hydropiperoides* Michx. | M | – | – | – | – | – | – |
| *Polygonum sagittatum* L. | H | – | – | 13 | 70 | <.5 | 5 |
| *Polygonum* spp. | L | – | – | – | – | – | – |
| *Pontederia cordata* L. | H | – | – | – | – | – | – |
| *Potamogeton pectinatus* L. | M | 1 | 11 | – | – | – | – |
| | L | 5 | 28 | – | – | – | – |
| *Ranunculus flabellaris* Raf. | H | 1 | 13 | – | – | – | – |
| | M | 1 | 19 | – | – | – | – |
| | L | 9 | 13 | – | – | – | – |
| *Rhus radicans* L. | H | <.5 | 3 | – | – | – | – |
| *Rumex crispus* L. | M | – | – | – | – | 1 | 5 |
| *Sagittaria latifolia* Willd. | H | – | – | 2 | 25 | – | – |
| | M | 1 | 7 | <.5 | 10 | – | – |
| | L | 1 | 9 | – | – | – | – |
| *Scirpus atrovirens* Willd. | H | – | – | 1 | 10 | – | – |

Table 1. Continued.

| Species | Zone | Hatfield 1974 C | Hatfield 1974 F | Hatfield 1984 C | Hatfield 1984 F | Ned's Ditch 1974 C | Ned's Ditch 1974 F |
|---|---|---|---|---|---|---|---|
| *Scutellaria lateriflora* L. | H | <.5 | 14 | <.5 | 4 | – | – |
| | M | <.5 | 2 | – | – | – | – |
| | L | <.5 | 2 | – | – | – | – |
| *Sium suave* Walt. | H | 1 | 5 | – | – | <.5 | 8 |
| | M | 1 | 10 | <.5 | 1 | <.5 | 3 |
| | L | – | – | – | – | – | – |
| *Solanum dulcamara* L. | M | <.5 | 2 | – | – | – | – |
| | L | <.5 | 2 | – | – | – | – |
| *Solidago* spp. | H | <.5 | 1 | – | – | – | – |
| | M | <.5 | 2 | – | – | – | – |
| *Sparganium americanum* Nutt. | M | – | – | – | – | – | – |
| | L | – | – | – | – | <.5 | 4 |
| *Sparganium androcladum* (Engelm.) Morong | M | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Spirodela polyrhiza* (L.) Schleid. | H | <.5 | 4 | <.5 | 8 | <.5 | 4 |
| | M | 2 | 68 | 1 | 43 | 1 | 60 |
| | L | 1 | 33 | <.5 | 33 | <.5 | 29 |
| *Symplocarpus foetidus* (L.) Nutt. | H | <.5 | 1 | <.5 | 1 | – | – |
| | M | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Taraxacum officinale* Weber | H | <.5 | 3 | – | – | – | – |
| *Thalictrum polygamum* Muhl. | H | – | – | 1 | 14 | – | – |

Table 1. Continued.

| Species | Zone | Ned's Ditch 1984 C | Ned's Ditch 1984 F | Whately 1974 C | Whately 1974 F | Whately 1984 C | Whately 1984 F |
|---|---|---|---|---|---|---|---|
| *Scutellaria lateriflora* L. | H | – | – | 1 | 15 | – | – |
| | M | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Sium suave* Walt. | H | 1 | 10 | <.5 | 5 | – | – |
| | M | 6 | 44 | – | – | – | – |
| | L | 1 | 9 | – | – | – | – |
| *Solanum dulcamara* L. | M | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Solidago* spp. | H | – | – | – | – | – | – |
| | M | – | – | – | – | – | – |
| *Sparganium americanum* Nutt. | M | 3 | 26 | – | – | – | – |
| | L | 1 | 9 | – | – | – | – |
| *Sparganium androcladum* (Engelm.) Morong | M | – | – | 7 | 40 | 13 | 35 |
| | L | – | – | 17 | 35 | 2 | 20 |
| *Spirodela polyrhiza* (L.) Schleid. | H | – | – | – | – | – | – |
| | M | <.5 | 39 | 2 | 50 | – | – |
| | L | <.5 | 19 | <.5 | 30 | – | – |
| *Symplocarpus foetidus* (L.) Nutt. | H | – | – | – | – | 6 | 15 |
| | M | – | – | 1 | 5 | 20 | 50 |
| | L | – | – | – | – | 2 | 5 |
| *Taraxacum officinale* Weber | H | – | – | – | – | – | – |
| *Thalictrum polygamum* Muhl. | H | – | – | – | – | – | – |

Table 1. Continued.

| Species | Zone | Hatfield 1974 C | Hatfield 1974 F | Hatfield 1984 C | Hatfield 1984 F | Ned's Ditch 1974 C | Ned's Ditch 1974 F |
|---|---|---|---|---|---|---|---|
| *Thelypteris palustris* Schott | H | – | – | – | – | – | – |
| | M | – | – | <.5 | 1 | – | – |
| *Typha latifolia* L. | H | – | – | <.5 | 8 | – | – |
| | M | – | – | <.5 | 6 | – | – |
| *Urtica dioica* L. | M | – | – | – | – | – | – |
| *Utricularia vulgaris* L. | M | – | – | – | – | <.5 | 7 |
| | L | – | – | – | – | 2 | 8 |
| *Vallisneria americana* Michx. | L | – | – | – | – | – | – |
| *Verbena hastata* L. | H | – | – | – | – | – | – |
| *Vitis* spp.[2] | H | 7 | 29 | 1 | 3 | 17 | 32 |
| | M | 1 | 5 | – | – | 1 | 6 |
| *Wolffia columbiana* Karst. | H | – | – | <.5 | 5 | – | – |
| | M | 1 | 40 | <.5 | 39 | – | – |
| | L | <.5 | 20 | <.5 | 45 | – | – |
| Shrubs and woody seedlings | | | | | | | |
| *Acer rubrum* L. | H | <.5 | 1 | <.5 | 6 | – | – |
| *Acer saccharinum* L. | H | <.5 | 14 | 1 | 36 | <.5 | 18 |
| | M | <.5 | 2 | – | – | <.5 | 4 |
| *Alnus rugosa* (DuRoi) Spreng | H | 1 | 6 | – | – | – | – |
| *Cephalanthus occidentalis* L. | H | 1 | 4 | 2 | 9 | <.5 | 8 |
| | M | <.5 | 2 | 2 | 3 | 68 | 83 |
| | L | <.5 | 2 | – | – | – | – |

Table 1. Continued.

| Species | Zone | Ned's Ditch 1984 C | Ned's Ditch 1984 F | Whately 1974 C | Whately 1974 F | Whately 1984 C | Whately 1984 F |
|---|---|---|---|---|---|---|---|
| *Thelypteris palustris* Schott | H | 5 | 26 | – | – | – | – |
| | M | – | – | – | – | – | – |
| *Typha latifolia* L. | H | – | – | 5 | 35 | – | – |
| | M | – | – | 16 | 40 | – | – |
| *Urtica dioica* L. | M | – | – | – | – | 1 | 5 |
| *Utricularia vulgaris* L. | M | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Vallisneria americana* Michx. | L | – | – | – | – | 1 | 15 |
| *Verbena hastata* L. | H | – | – | 1 | 10 | – | – |
| *Vitis* spp.[2] | H | 8 | 29 | 1 | 10 | – | – |
| | M | – | – | – | – | – | – |
| *Wolffia columbiana* Karst. | H | – | – | – | – | – | – |
| | M | <.5 | 6 | – | – | <.5 | 20 |
| | L | <.5 | 7 | – | – | <.5 | 40 |
| Shrubs and woody seedlings | | | | | | | |
| *Acer rubrum* L. | H | – | – | – | – | – | – |
| *Acer saccharinum* L. | H | 3 | 29 | – | – | – | – |
| | M | <.5 | 2 | – | – | – | – |
| *Alnus rugosa* (DuRoi) Spreng | H | – | – | 1 | 10 | – | – |
| *Cephalanthus occidentalis* L. | H | 6 | 14 | – | – | – | – |
| | M | 22 | 41 | – | – | – | – |
| | L | – | – | – | – | – | – |

Table 1. Continued.

| Species | Zone | Hatfield 1974 C | Hatfield 1974 F | Hatfield 1984 C | Hatfield 1984 F | Ned's Ditch 1974 C | Ned's Ditch 1974 F |
|---|---|---|---|---|---|---|---|
| *Cornus amomum* Mill. | H | 3 | 21 | 5 | 18 | – | – |
| | M | 1 | 2 | <.5 | 4 | – | – |
| *Cornus stolonifera* Michx. | H | – | – | – | – | 23 | 44 |
| | M | – | – | – | – | 1 | 4 |
| *Decodon verticillatus* (L.) Ell. | H | 1 | 10 | 2 | 5 | – | – |
| | M | 28 | 62 | 10 | 43 | – | – |
| | L | 2 | 13 | 1 | 12 | – | – |
| *Ilex verticillata* (L.) Gray | H | – | – | – | – | 1 | 4 |
| *Prunus* sp. | H | <.5 | 1 | – | – | – | – |
| *Quercus coccinea* Muenchh. | H | – | – | – | – | – | – |
| *Quercus palustris* Muenchh. | H | – | – | – | – | – | – |
| *Rosa palustris* Marsh. | H | – | – | <.5 | 1 | – | – |
| *Rubus* spp. | H | – | – | – | – | – | – |
| *Salix* spp. | H | <.5 | 1 | 1 | 1 | <.5 | 2 |
| | M | – | – | – | – | – | – |
| | L | <.5 | 2 | – | – | <.5 | 11 |
| *Sambucus canadensis* L. | H | – | – | – | – | – | – |
| *Spiraea latifolia* (Ait.) Borkh. | H | – | – | – | – | – | – |
| *Ulmus rubra* Muhl. | H | <.5 | 1 | <.5 | 1 | – | – |
| | M | – | – | <.5 | 3 | – | – |

Table 1. Continued.

| Species | Zone | Ned's Ditch 1984 C | Ned's Ditch 1984 F | Whately 1974 C | Whately 1974 F | Whately 1984 C | Whately 1984 F |
|---|---|---|---|---|---|---|---|
| *Cornus amomum* Mill. | H | – | – | – | – | <.5 | 5 |
| | M | – | – | – | – | 1 | 5 |
| *Cornus stolonifera* Michx. | H | 6 | 27 | – | – | – | – |
| | M | – | – | – | – | – | – |
| *Decodon verticillatus* (L.) Ell. | H | <.5 | 1 | – | – | – | – |
| | M | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Ilex verticillata* (L.) Gray | H | <.5 | 3 | – | – | – | – |
| *Prunus* sp. | H | – | – | <.5 | 5 | – | – |
| *Quercus coccinea* Muenchh. | H | – | – | <.5 | 5 | – | – |
| *Quercus palustris* Muenchh. | H | 1 | 7 | – | – | – | – |
| *Rosa palustris* Marsh. | H | – | – | 3 | 15 | – | – |
| *Rubus* spp. | H | – | – | – | – | <.5 | 5 |
| *Salix* spp. | H | – | – | 3 | 10 | – | – |
| | M | – | – | – | – | – | – |
| | L | – | – | – | – | – | – |
| *Sambucus canadensis* L. | H | – | – | 1 | 10 | 1 | 5 |
| *Spiraea latifolia* (Ait.) Borkh. | H | – | – | 1 | 10 | – | – |
| *Ulmus rubra* Muhl. | H | – | – | – | – | – | – |
| | M | – | – | – | – | – | – |

Table 1. Continued.

| Species | Zone | Hatfield 1974 C | Hatfield 1974 F | Hatfield 1984 C | Hatfield 1984 F | Ned's Ditch 1974 C | Ned's Ditch 1974 F |
|---|---|---|---|---|---|---|---|
| *Viburnum recognitum* Fern. | H | – | – | 1 | 5 | 5 | 10 |
| | M | – | – | – | – | <.5 | 1 |
| Total species | H | 47 | | 42 | | 29 | |
| | M | 30 | | 29 | | 17 | |
| | L | 21 | | 14 | | 10. | |
| % Cover | H | 78 | | 74 | | 82 | |
| | M | 122 | | 65 | | 78 | |
| | L | 51 | | 56 | | 17 | |

[1] Includes identifiable *C. intumescens* Rudge at Whately (1974), *C. stricta* Lam. at Hatfield (1984), and *C. tribuloides* Wahlenb. at Hatfield (1974, 1984).

[2] Mostly *V. riparia* Michx.

Table 1. Continued.

| Species | Zone | Ned's Ditch 1984 C | Ned's Ditch 1984 F | Whately 1974 C | Whately 1974 F | Whately 1984 C | Whately 1984 F |
|---|---|---|---|---|---|---|---|
| *Viburnum recognitum* Fern. | H | 1 | 4 | — | — | — | — |
| | M | — | — | — | — | 1 | 5 |
| Total species | H | 28 | | 38 | | 19 | |
| | M | 14 | | 21 | | 14 | |
| | L | 10 | | 5 | | 8 | |
| % Cover | H | 88 | | 104 | | 81 | |
| | M | 50 | | 76 | | 68 | |
| | L | 30 | | 32 | | 32 | |

Table 2. The Simpson Index of Resemblance comparing selected floras of the oxbow marshes and 1973–1975 swamp forest herb strata (SFHS) at the specific level.

| Floras Compared | Resemblance |
|---|---|
| Hatfield marsh 1974/Hatfield marsh 1984 | 69.2 |
| Ned's Ditch marsh 1974/Ned's Ditch marsh 1984 | 78.1 |
| Whately marsh 1974/Whately marsh 1984 | 44.4 |
| Hatfield marsh 1974/Hatfield SFHS | 60.0 |
| Ned's Ditch marsh 1974/Ned's Ditch SFHS | 75.8 |
| Whately marsh 1974/Whately SFHS | 6.9 |
| Hatfield marsh 1984/Hatfield SFHS | 51.9 |
| Ned's Ditch marsh 1984/Ned's Ditch SFHS | 69.7 |
| Whately marsh 1984/Whately SFHS | 7.4 |
| Hatfield marsh 1974/Ned's Ditch marsh 1974 | 60.6 |
| Ned's Ditch marsh 1974/Whately marsh 1974 | 39.4 |
| Hatfield marsh 1974/Whately marsh 1974 | 48.8 |
| Hatfield marsh 1984/Ned's Ditch marsh 1984 | 65.6 |
| Ned's Ditch marsh 1984/Whately marsh 1984 | 40.7 |
| Hatfield marsh 1984/Whately marsh 1984 | 63.0 |
| Hatfield SFHS/Ned's Ditch SFHS | 36.0 |
| Ned's Ditch SFHS/Whately SFHS | 13.0 |
| Hatfield SFHS/Whately SFHS | 21.0 |
| Whately marsh 1974/Hatfield SFHS | 53.5 |
| Whately marsh 1974/Ned's Ditch SFHS | 34.9 |
| Whately marsh 1984/Hatfield SFHS | 40.7 |
| Whately marsh 1984/Ned's Ditch SFHS | 29.6 |
| Hatfield marsh 1974/Ned's Ditch SFHS | 40.0 |
| Hatfield marsh 1984/Ned's Ditch SFHS | 36.0 |
| Ned's Ditch marsh 1974/Hatfield SFHS | 45.5 |
| Ned's Ditch marsh 1984/Hatfield SFHS | 40.6 |

high, mid, and low marsh at each sampling period, and to compare the floras of the marshes with the floras of the herb strata of adjacent oxbow swamp forests during the period 1973–1975 (data from Holland and Burk, 1984). Simpson's Index of Resemblance (100 c/n1 in which c is the number of species common to the two floras and n1 the total number of species in the smaller flora) has been used in previous comparisons within the New England flora (Lauermann and Burk, 1976; Holland and Sorrie, 1989). The index seems particularly useful when floras of approximately equal sizes occurring in a common area are compared.

Additional marsh species observed and collected at the sites but never sampled are listed in Sackett (1974, op. cit.; 1977, op.

cit.); most of these species are uncommon to rare and occur in transitional or disturbed habitats at the edges of the marshes. Data representing specimens of *Carex, Polygonum, Prunus, Rubus, Salix,* and *Solidago* that could not be identified to species are grouped under each genus in the tables. For purposes of consistency, nomenclature follows Fernald (1950) except in the cases of (1) *Matteuccia,* which is conserved over *Pteretis* as used in that manual, (2) *Thelypteris,* now generally accepted as the genus of the marsh fern, *T. palustris,* which Fernald included in *Dryopteris,* and (3) *Bidens tripartita* L. to include *B. comosa* and *B. connata.* Authorities of all known species discussed herein are given in Table 1. Specimens of all taxa collected have been deposited in SCH.

## RESULTS AND DISCUSSION

### General Observations

Metzler and Damman (1985) have documented marked annual changes in the vegetation of certain floodplain habitats, particularly undrained sloughs, as a result of varying flood patterns in the lower reaches of the Connecticut River. The Massachusetts oxbow habitats, which are upstream from natural tidal influences, show more predictable year-to-year relationships. Comparisons of the Simpson Index of Resemblance indicate that the floras of the Ned's Ditch marshes showed the least change over the interval 1974–1979 (Table 2). Somewhat greater change occurred in the floras of the Hatfield marshes, while the Whately marshes changed quite drastically.

The herbaceous strata of the oxbow swamp forests are distinctive, with relatively few species occurring in all three oxbows (Holland and Burk, 1984). This uniqueness of the individual swamp forest floras is reflected in their relatively low similarities of resemblance (Table 2). Overall, the floras of the marshes of the three oxbows are more similar to one another than to the floras of the adjacent swamp forests. This similarity increased slightly over the period 1974–1984 (Table 2); a group of species that includes *Apios americana, Bidens tripartita, Boehmeria cylindrica, Leersia oryzoides, Lemna minor, Ludwigia palustris, Nuphar variegatum, Onoclea sensibilis, Sagittaria latifolia, Sium suave, Spirodela polyrhiza, Viburnum recognitum, Vitis riparia,*

and *Wolffia columbiana* was sampled in all three marshes during at least one sampling period.

The high marsh zones of the three oxbows tend to be most similar to one another (Sackett, 1977, op. cit.). This similarity at Hatfield and Ned's Ditch has persisted for a decade, while, with the increasing abundance of *Onoclea sensibilis,* high marsh at Whately increasingly resembles that of the other two oxbows. The low marsh zones of the three oxbows, dominated by varying proportions of *Lemna minor* and *Nuphar variegatum,* are also similar, but mid marsh emergent plant communities have remained distinctive at each oxbow through the study period.

Total cover and species richness were usually highest in high marsh and lowest in low marsh; the exceptions to this were observed during the relatively dry summer of 1974 when crowded populations of *Lemna minor* filled the mid marsh at Hatfield and heavy growth of *Cephalanthus occidentalis* shaded adjacent high marsh at Ned's Ditch.

## The Hatfield Oxbow

Swamp forests adjacent to the Hatfield marshes are dominated by an overstory of *Populus deltoides* in association with *Acer saccharinum,* arborescent *Alnus rugosa,* and smaller specimens of *Acer negundo, A. rubrum, Fraxinus pensylvanica, Salix nigra,* and other trees. *Populus deltoides* is not regenerating and will probably be replaced by more shade-tolerant species.

The flora of the Hatfield marsh shows a strong similarity to the flora of the herb strata of the Hatfield swamp forest (Table 2). Over three-fourths of the 40 herbaceous species sampled in the understory of the swamp forest in 1974 and 1975 (Sackett, 1977 op. cit.; Holland and Burk, 1982) also occurred in the Hatfield marshes (34 species in 1974, 32 in 1984). Species that were present in the marsh in 1974 but absent in 1984 included typical swamp forest species such as *Convolvulus sepium, Echinocystis lobata,* and *Maianthemum canadense*; these were originally present with low coverage and frequencies. Similarly, several species that were "new" to the marsh in 1984, including *Amphicarpa bracteata, Arisaema triphyllum,* and *Thalictrum polygamum,* were also more commonly associated with the swamp forest herb strata. We had previously observed that a number of emergent marsh species of the oxbows occur with high frequency but low cover in the herb

strata of the Hatfield forest (Holland and Burk, 1984). In addition, some species were of nearly equal abundance and/or frequency in the forest and the marsh.

HIGH MARSH. High marsh at Hatfield contained more species than any zone of any other marsh sampled through the period. Most high marsh species could be included in one of three broad categories: (1) herbaceous annuals and perennials, many of which also occurred in the adjacent swamp forest, (2) vines, which are characteristic of the herb stratum of swamp forest both at Hatfield and in floodplain forests elsewhere on the Connecticut River (Nichols, 1916), and (3) woody seedlings of swamp forest trees and shrubs. During the 1974–1984 interval, herbaceous species fluctuated in abundance. Vines declined in high marsh, while the coverage and frequency of most species represented by woody seedlings increased. Actual (unrounded) cover values of *Acer rubrum,* for example, rose from 0.02% to 0.11% in the interval while cover values of *A. saccharinum* rose from 0.20 to 1.15%. Larson and Golet (1982) noted that succession from shallow marsh (equivalent to our high marsh) to forested wetlands involves a simple "replacement of one dominant life form by another" and not a major change in the hydrological regime. The increase in woody seedlings in the Hatfield high marsh may suggest the initial stages of this replacement here.

*Onoclea sensibilis* dominated high marsh on all eight baselines in 1974 and all but one in 1984. Two vines, *Apios americana* and *Vitis riparia,* together contributed slightly more than 10% cover to the high marsh in 1974 and sightly less in 1984.

MID MARSH. *Lemna minor* covered over half the water surface in the Hatfield mid marsh during the relatively dry summer of 1974, often forming a separate stratum beneath emergent vegetation. *Decodon verticillatus* was the most prominent emergent, followed in order of decreasing abundance by *Leersia oryzoides* and *Peltandra virginica.*

In the freshwater tidal lower reaches of the Connecticut River, Metzler and Damman (1985) found *Peltandra virginica* the most abundant species in herbaceous marsh communities within frequently flooded, low-lying swales, sometimes growing in association with *Leersia oryzoides.* At Hatfield by 1984, *Peltandra virginica* had become the dominant emergent. *Decodon verticillatus* remained important, but *Leersia oryzoides* was surpassed in abundance by *Lemna minor, Decodon verticillatus,* and *Onoclea sen-*

*sibilis* on the single baseline it had dominated ten years earlier. *Lemna minor* was much less abundant, possibly because of strong currents associated with the late May flood; total vegetative cover decreased correspondingly.

LOW MARSH. In 1974, *Lemna minor* and *Nuphar variegatum* together covered more than one-third of the open water surface in low marsh at the Hatfield oxbow. Little vegetation occurred along three baselines. Submerged aquatics, including *Cabomba caroliniana* in association with *Ceratophyllum demersum* and *Elodea nuttallii,* provided slightly less than 10% cover below the water surface.

In 1984, *Lemna minor* and *Nuphar variegatum* were still dominant, and one sparsely vegetated baseline had been colonized by *Nymphaea odorata* and *Nuphar variegatum.* The abundances of *Cabomba caroliniana* and *Ceratophyllum demersum* were little changed, but *Elodea nuttallii* was absent. The first Massachusetts collections of *Cabomba caroliniana* were made in South Pond, the lower segment of the Hatfield oxbow, in 1930 (Manning, 1937). *Cabomba caroliniana* had been observed at that site since the early 1920's and has become generally widespread elsewhere in New England in the interval (Burk et al., 1976; Hellquist and Crow, 1984).

**Ned's Ditch**

The nine ponds containing marsh vegetation at Ned's Ditch are effectively separated during much of the year by more continuous stands of swamp forest and buttonbush (*Cephalanthus occidentalis*) swamp. During intervals of flooding, high water extends throughout the forest, swamp, and marshes. Nonetheless, Ned's Ditch is the only one of the three study sites that does not receive regular flow from a source other than the Connecticut River, and during periods of drought, some or all of the ponds may dry out. During September of 1980, for example, we observed that all of the ponds except for the two sections of the old Mill River bed completely lacked standing water; later that season what had been formerly low marsh and open water supported dense fruiting stands of *Bidens* spp.

The swamp forest at Ned's Ditch is older, more extensive, and better developed than the swamp forest at Hatfield, and is dominated by *Acer saccharinum* in association with *Quercus palustris*

and *Fraxinus pensylvanica.* The overall resemblance between the Ned's Ditch marshes and the herbaceous stratum of the Ned's Ditch swamp forest is nearly as high as the resemblance between the Ned's Ditch marsh floras at the two sampling intervals (Table 2). Most species of the Ned's Ditch marshes also occur in the adjacent forests, where they vary in abundance from year to year in apparent response to fluctuating water levels (Holland and Burk, 1984). The dynamic interaction of marsh and swamp forest vegetation is exemplified by the distribution within the oxbow of *Ludwigia polycarpa,* currently on the threatened list in Massachusetts (Sorrie, 1987). *Ludwigia polycarpa* was present in the high marsh in 1974 and became established in adjacent swamp forest quadrats by 1975; it had disappeared from high marsh by 1984 but persisted in the forest, becoming re-established in the marsh in 1985 (M. M. Holland, pers. obs.).

Table 3 lists the dominant taxa of high, mid, and low marsh in each of the nine Ned's Ditch ponds in 1974 and in 1984. Most changes in dominance probably resulted from variations in water level throughout the study period and do not reflect long-term trends of marsh development.

HIGH MARSH. In 1974, *Cornus stolonifera, Vitis riparia,* and *Onoclea sensibilis* were the most important high marsh species in order of decreasing abundance (Table 1). Only *Osmunda regalis* also occurred at cover greater than 5%. Four ponds lacked a zone of high marsh, probably as a result of heavy shading by adjacent stands of buttonbush swamp. *Cornus stolonifera* dominated high marsh at two ponds, *Osmunda regalis* at one, *Onoclea sensibilis* at one, and *Onoclea sensibilis* overlain with vines of *Vitis riparia* at one (Table 3).

By 1984, *Onoclea sensibilis* and *Osmunda regalis* had increased to become the most prominent high marsh species, while *Cornus stolonifera* and *Vitis riparia* declined (Table 1). Throughout Ned's Ditch, *Cephalanthus occidentalis* had been damaged by the late May flood. A high marsh dominated by *Osmunda regalis* had developed in one pond where high marsh had previously been lacking, and a similar new high marsh dominated by *Onoclea sensibilis* had developed in another; two ponds still lacked high marsh (Table 3). *Cornus stolonifera* retained dominance at one pond but at the other was surpassed by *Onoclea sensibilis, Osmunda regalis,* and other species. *Osmunda regalis, Onoclea sensibilis,* and *Onoclea sensibilis/Vitis riparia* remained dominant in

Table 3. Dominant taxa of high, mid, and low marsh in each of the 9 Ned's Ditch ponds in 1974 and 1984. For ease of comparison, only generic names are listed; see text for species occurring and pond locations. The notation "sparse veg." indicates the zone supported only scanty plant cover or open water; "no zone" indicates the zone was absent.

| Pond # | Year | High Marsh | Mid Marsh | Low marsh |
|---|---|---|---|---|
| 1 | 1974 | *Osmunda* | *Osmunda* | *Nuphar* |
| | 1984 | *Osmunda* | *Sium/Sparganium* | *Nuphar* |
| 2 | 1974 | no zone | *Cephalanthus* | *Nuphar* |
| | 1984 | *Osmunda* | *Cephalanthus* | *Nuphar* |
| 3 | 1974 | *Onoclea* | *Cephalanthus* | *Nuphar* |
| | 1984 | *Onoclea* | *Cephalanthus* | *Nuphar* |
| 4 | 1974 | no zone | *Cephalanthus* | sparse veg. |
| | 1984 | *Onoclea* | *Cephalanthus* | *Ranunculus* |
| 5 | 1974 | *Cornus* | no zone | *Potamogeton* |
| | 1984 | *Onoclea* | *Leersia* | sparse veg. |
| 6 | 1974 | no zone | *Cephalanthus* | sparse veg. |
| | 1984 | no zone | *Bidens* | sparse veg. |
| 7 | 1974 | no zone | *Cephalanthus* | *Nuphar* |
| | 1984 | no zone | *Bidens* | *Nuphar* |
| 8 | 1974 | *Onoclea/Vitis* | *Cephalanthus* | *Nuphar* |
| | 1984 | *Onoclea/Vitis* | *Nuphar* | *Nuphar* |
| 9 | 1974 | *Cornus* | no zone | *Nuphar* |
| | 1984 | *Cornus* | *Nuphar* | *Potamogeton* |

ponds where dominant in 1974. *Bidens* spp., *Thelypteris palustris, Dulichium arundinaceum,* and seedlings of *Acer saccharinum* had all increased by 1984 to occupy high marsh in at least five ponds.

MID MARSH. In 1974, *Cephalanthus occidentalis* occupied 68% of the sampled area (Table 1) and dominated mid marsh at six ponds (Table 3). *Osmunda regalis* was dominant at one pond, while two ponds lacked mid marsh.

In 1984, *Cephalanthus occidentalis,* despite a sharp decline in cover (Table 1) retained dominance in three ponds, but was replaced as dominant by *Bidens* spp. in two ponds and by *Nuphar variegatum* in the other. In one pond, *Sium suave* and *Sparganium americanum* in nearly equal abundance had replaced *Osmunda regalis* as dominant. *Nuphar variegatum* had established a new zone of mid marsh in one pond as had *Leersia oryzoides* in another (Table 3).

LOW MARSH. *Nuphar variegatum* was dominant in low marsh in six ponds in Ned's Ditch in 1974 and *Potamogeton pectinatus* in one; two ponds contained open water with only sparsely scat-

tered low marsh vegetation (Table 3). *Nuphar variegatum* continued to dominate five ponds in 1984 but was replaced as dominant in one by *Potamogeton pectinatus.* The zone of low marsh previously dominated by *P. pectinatus* contained only open water when sampled in 1984. *Ranunculus flabellaris* had increased overall and dominated one pond which had little low marsh vegetation earlier; the other pond contained only scattered *Lemna minor, Spirodela polyrhiza,* and *Wolffia columbiana.*

Throughout the study period, *Lemna minor* and *Spirodela polyrhiza* occurred regularly, though sparsely, in low marsh in most or all of the ponds. A third member of the Lemnaceae, *Wolffia columbiana,* was first collected in Massachusetts in the vicinity of Ned's Ditch in 1933 (Manning, 1934). However, this species was not observed anywhere in Ned's Ditch or in the adjacent sections of the Northampton oxbow during the period 1973–1975 (Burk, 1977; Sackett, 1977 op. cit.). *Wolffia columbiana* has recently become abundant at a number of western Massachusetts sites (Burk et al., 1976; Hellquist and Crow, 1982) and apparently invaded Ned's Ditch within the decade.

## The Whately Oxbow

Vegetational and floristic changes in the Whately marshes over the decade were marked by a sharp decline in species richness in high and mid marsh (Table 1). These changes could be attributed in part to human activities, including waste disposal, in the vicinity of the single pond. Marsh species at Whately are generally excluded from the adjacent swamp forests, which are dominated by *Acer rubrum* above an herb stratum comprised of ferns and spring-blooming herbs more typical of upland sites (Holland and Burk, 1984). As a result, resemblance between the Whately marshes and the herbaceous stratum of the Whately swamp forest is extremely low (Table 2). The 1974 flora of the Hatfield marsh did, however, show an unexpectedly high resemblance to the flora of the Hatfield swamp forest; this resemblance was lower in 1984 because of the loss of numerous species from the Whately marsh. Both the Hatfield and Ned's Ditch marshes were more similar throughout the study period to their adjacent swamp forests than to the swamp forests of the other oxbows (Table 2).

HIGH MARSH. In 1974, the high marsh at Hatfield was relatively diverse with a mixture of both annual and perennial species pres-

ent at cover values greater than 5%. The vegetation along the two transects differs substantially. On the northern transect, which crosses the only remaining ponded open water, the most abundant species in order of decreasing cover values (ranging from 15% to 7%) were *Juncus effusus, Agrostis alba, Typha latifolia, Onoclea sensibilis,* and *Leersia oryzoides.* All these were either absent or scantily represented in 1984 except *Onoclea sensibilis,* which had increased to occupy 41% of the zone.

In high marsh on the lower transect in 1974, *Polygonum sagittatum, Onoclea sensibilis, Carex intumescens,* and *Impatiens capensis* were most important with cover values ranging from 23% down to 11%. By 1984, cover of *Onoclea sensibilis* had increased to 71%, *Impatiens capensis* to 17%, and *Symplocarpus foetidus,* new to the zone, to 8%. Both *Carex intumescens* and *Polygonum sagittatum* had declined to cover values less than 0.5%.

Of the 39 high marsh taxa recorded at Whately in 1974, 25 species also occurred in the herb strata of swamp forest at either Hatfield or Ned's Ditch or both of these regularly flooded sites. Seventeen (68% of the total shared) had disappeared from the Whately marsh by 1984; since these were not replaced by other taxa, overall diversity decreased sharply.

Mid marsh. Mid marsh on the northern transect was dominated in 1974 by *Typha latifolia* with *Lemna minor* second in abundance. In 1984, *Typha latifolia* was absent, replaced in part by *Sparganium androcladum. Lemna minor* was less abundant; species richness had dropped from ten to four.

*Leersia oryzoides,* with 34% cover, dominated mid marsh on the lower transect in 1974, followed in abundance by *Impatiens capensis* and *Sparganium androcladum.* In 1984, *Symplocarpus foetidus* was dominant, followed in abundance by *Impatiens capensis* and *Onoclea sensibilis. Leersia oryzoides* and *Sparganium androcladum* were no longer present in the zone.

Low Marsh. *Nuphar variegatum* dominated low marsh on the northern transect in 1974 and by 1984 had increaed in combination with newly established *Nymphaea odorata* to occupy over 52% of the surface. *Lemna minor* and *Spirodela polyrhiza* occurred sparsely in this zone in 1974; by 1984, *Spirodela polyrhiza* had disappeared, but at Ned's Ditch, *Wolffia columbiana,* previously absent, had invaded.

Low marsh on the lower transect was dominated by *Sparga-*

*nium androcladum* in association with *Impatiens capensis, Lemna minor,* and *Spirodela polyrhiza* in 1974. By 1984, *Sparganium androcladum* had declined to 4% cover; *Lemna minor, Impatiens capensis,* and *Spirodela polyrhiza* were absent; and *Myosotis scorpioides, Symplocarpus foetidus,* and *Vallisneria americana* were present at cover values of 3% or lower.

## Conservation

ROLE OF EXOTIC SPECIES. The invasions and subsequent spread of non-native species have classically been considered both causes and effects of habitat disruption. In the marshes of the southeastern portion of the prehistoric Northampton oxbow and throughout two ponds within Arcadia Wildlife Sanctuary, several non-native species including *Iris pseudacorus* L., *Lythrum salicaria,* and *Marsilea quadrifolia* L. are common and considered "management concerns" by the wildlife sanctuary staff (McGuire, 1989). However non-native species as a group (excluding the two spreading indigenous species, *Cabomba caroliniana* and *Wolffia columbiana*) are not abundant in the oxbow marshes included in this study. *Lysimachia nummularia,* a minor component of the Ned's Ditch marsh throughout the study period, is an important component of the herb stratum of the Hatfield swamp forest (Table 1). A few non-natives including *Glechoma hederacea, Solanum dulcamara,* and *Taraxacum officinale* were collected in 1974 but not in 1984 and may be regarded as transitory colonists of marsh habitats. *Lythrum salicaria,* a species which has been identified as a "serious threat to native emergent vegetation in shallow-water marshes throughout the northeastern and north-central region" (Thompson et al., 1987) was sampled in the Hatfield high and mid marshes in 1974 but not in 1984. However, *Lythrum salicaria* is now abundant in a disturbed section of the Hatfield oxbow adjacent to a feedlot and road embankment (C. J. Burk, pers. obs. through 1989).

PRESERVATION. We have previously stressed the importance of protection for oxbow habitats (Burk and Holland, 1979; Holland and Burk, 1984). Marsh zones within riparian systems have traditionally been recognized both as discrete communities and as ecotones, the transitions between adjacent plant communities (Holland et al., 1990). Ecotones often contribute extensively to biotic diversity within a region since they frequently support, in

addition to species characteristic of the verging communities, species uniquely adapted to the ecotone environment (see di Castri et al., 1988, for a recent review of this topic.) The Massachusetts oxbow marshes represent a unique phase in the transition between the open water of the former river bed and floodplain forest. Their extent is inversely proportional to the age of the oxbow itself, and they contain in many instances relics of formerly more widespread floras and vegetation types. At present, only the prehistoric Northampton oxbow is fully protected as a natural area. Both the Hatfield and Whately oxbows are for the most part privately owned and potentially subject to extensive further disturbance by human activities. Their preservation in a natural state, free of disrupting human influences, demands high management priority.

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# NEW ENGLAND NOTE

# TWO RARE TAXA REDISCOVERED AT MT. TOM, HOLYOKE, HAMPDEN CO., MASSACHUSETTS

ANDREW H. WILLIAMS

**ABSTRACT**

In 1989, *Oxalis violacea* and *Verbena simplex* were rediscovered at Mt. Tom, Holyoke, Hampden Co., Massachusetts, where they were last recorded in 1880. *Oxalis violacea* is listed as Threatened and *Verbena simplex* as Endangered by the state of Massachusetts.

Key Words: Flora, endangered, threatened, Massachusetts

In 1989, *Oxalis violacea* L. and *Verbena simplex* Lehm. were rediscovered at Mt. Tom, Holyoke, Hampden Co., Massachusetts, and specimens have been deposited at SCHN. *Oxalis violacea* and *Verbena simplex* were last recorded at Mt. Tom by S. Stebbins whose specimens, dated 1880 and July 21, 1880 respectively, are in the Springfield Science Museum Herbarium.

*Oxalis violacea* was rediscovered May 29, 1989, on a steep and very rocky site on the eastern slope of the basaltic upper region of Mt. Tom. Toward the south end of Mt. Tom are dry oak-hickory woods with an understory dominated by *Gaylussacia baccata* (Wang.) K. Koch, *Vaccinium angustifolium* Ait., *V. pallidum* Ait., and *V. stamineum* L. In this area, some intermittent wetness is apparent by the contours of the land. The presence of *Geranium maculatum* L., *Staphylea trifolia* L., and *Acer saccharum* Marsh., which are not generally distributed on basalt toward the south end of Mt. Tom, is here restricted to these moist sites. Other associates were *Dryopteris marginalis* (L.) Gray, *Hystrix patula* Moench, *Carex flaccosperma* Dewey var. *glaucodea* (Tuckerman) Kukenth. (itself listed as Endangered in Massachusetts), *Hypoxis hirsuta* (L.) Coville, *Polygonatum pubescens* (Willd.) Pursh, *Ostrya virginiana* (P. Mill.) K. Koch, *Thalictrum revolutum* DC., *T. thalictroides* (L.) Eames & Boivin, *Vaccinium stamineum* L., *Lysimachia quadrifolia* L., *Fraxinus americana* L., *Asclepias quadrifolia* Jacq., *Pycnanthemum muticum* (Michx.) Pers., and *Conopholis americana* (L.) Wallr.

One fallen flower of *Oxalis* was the sole evidence of flowering. Approximately seventy-five plants are present in an area of about

100 m² in the configuration of water runoff. At present, two other sites are known for this species in Massachusetts, where it is classified as Threatened by the state. One site is on the Mt. Holyoke Range, Hampshire Co., just across the Connecticut River, and one site is in Concord, Middlesex Co. (Sorrie, 1987).

*Verbena simplex* was rediscovered September 9, 1989, on a steep open slope on the southeast flank of the mountain. There is much exposed basalt, and plants of *V. simplex* grow in crevices and on small ledges. Many basalt balds occur on Mt. Tom, but this site is unusual in that it supports *Andropogon gerardii* Vitman, a grass which also grows at the summit of Mt. Tom. This grass needs more water than does *Schizachyrium scoparium* (Michx.) Nash (Weaver, 1954) which is very widespread at Mt. Tom and which is also present at this site. Other associates include *Woodsia ilvensis* (L.) R. Br., *Juniperus virginiana* L., *Danthonia spicata* (L.) Beauv., *Polygonum scandens* L., *Corydalis sempervirens* (L.) Pers., *Spiraea latifolia* (Ait.) Borkh., *Lespedeza virginica* (L.) Britt., *Rhus typhina* L., *Viola fimbriatula* Sm., *Fraxinus americana* L., *Hedeoma pulegioides* (L.) Pers., *Pycnanthemum muticum* (Michx.) Pers., *Trichostema dichotomum* L., *Agalinis tenuifolia* (Vahl) Raf., *Aureolaria pedicularia* (L.) Raf., *Aster solidagineus* Michx., *Solidago bicolor* L., and *S. nemoralis* Ait.

*Verbena simplex* was still flowering when discovered. Several plants are present in an area of only about 3 m². At present, one other site is known for this Endangered species in Massachusetts: on the wall of an abandoned marble quarry in Sheffield, Berkshire Co. (Sorrie, 1987).

## ACKNOWLEDGMENTS

I am grateful to C. John Burk, Bruce Sorrie, Bill Kenney and Marian Rohman for their support of my Mt. Tom flora project.

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RHODORA, Vol. 92, No. 871, pp. 207–208, 1990

# BOOK REVIEW

William J. Cody and Donald M. Britton. 1989. *Ferns and Fern Allies of Canada.* Pp. iv + 430; illustrated. Agriculture Canada, Ottawa. Available from Canadian Government Publishing Centre, Supply and Services Canada, Ottawa, Canada K1A 0S9. (Softbound, also in French.) ISBN 0-660-13102-1.

Large-scale fern floras for various parts of the New World have been appearing at a rapid rate in recent years, though the date of their conception varies widely. Floras are now in place for the United States, two states of Mexico, Guatemala, the Lesser Antilles, and Jamaica; partially published for Costa Rica and Peru; and likely to appear in the foreseeable future for Hispaniola, Puerto Rico, Mesoamerica, and North America. The prospect of a hemisphere documented by fern floras does not seem impossible, especially with the appearance of this fern flora for Canada, which provides us with concise, modern documentation of the pteridophyte flora for the boreal portion of the New World.

Canada's is not a rich fern flora: 140 species of ferns and other spore-dispersed plants are reported for an area of about 3.6 million square miles. Compare the state of Oaxaca, Mexico, from which Mickel and Beitel (1988) record 690 species (five times the diversity) from about 36,000 square miles (1/1000th the area). Nevertheless, this northern country has yielded some of the most interesting taxa in recent systematic studies, taxa that have revealed much about the evolutionary process among spore-dispersed plants in north-temperate areas. This basic manual provides us in very usable format a detailed reference work to the ferns of these northern lands, incorporating the vast majority of recent biosystematic work in the area.

In basic layout, the book comprises a full set of diagnostic keys as well as complete descriptions and illustrations of the species and subspecific taxa for the entire country. Information on habitat, chromosome number, and range complements the descriptive text for each taxon. An introduction, including a history of fern study in Canada and some basic biology of ferns relevant to field work and systematics, open the book. The treatment of species is traditional enough to be convenient but modern enough to be informative about species relationships, which makes the book

useful to a wide audience. In addition to the basic features, there are a number of aids that make this volume a particularly useful tool. Prominent and useful is a full set of distribution maps for the flora, included as a separate section in the book. Also noteworthy are the explanatory diagrams for the polyploid complexes in difficult genera such as *Dryopteris* and *Polystichum*. Two features of the text are particularly useful: the treatment of each genus begins with an introduction that includes notes on the difficulties encountered in the genus and ends with a review of the known hybrids (these, perhaps wisely, are not included in the keys). There is a helpful illustration on each taxon, and a glossary and references section are included at the end of the work.

The *Ferns and Fern Allies of Canada* bears imprints of a long history of development: both the introduction and literature cited have addenda, which would have been better merged with the main portion of the text. That the time invested in this work was nevertheless worth it is clear from this review.

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RHODORA, Vol. 92, No. 871, p. 209, 1990

# BOOK REVIEW

G. Barbour and William Dwight Billings, Eds. 1988. *North American Terrestrial Vegetation.* Pp. vii + 434; tables, illus. Cambridge University Press, Cambridge, U.K. (£45.00; $49.50)

The floras of North America have, for the most part, been relatively well studied as to their composition. As the editors say in their preface: "There is a rich heritage of texts on North American vegetation, and we stand on the shoulders of their authors in order to see just a bit farther."

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The audiences that this book may serve include taxonomists, conservationists, ecologists, foresters, certain commercially oriented organizations, several kinds of governmental institutions and many interested laymen. It could well serve as a text book in a variety of plant science courses for undergraduate and graduate students.

RICHARD EVANS SCHULTES
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CAMBRIDGE, MA 02138

# WORKSHOP ANNOUNCEMENT AND CALL FOR ABSTRACTS

# THE ATLANTIC COASTAL PLAIN FLORA: TOWARD A NORTH AMERICAN CONSERVATION STRATEGY

An international workshop on development of a conservation strategy for the Atlantic Coastal Plain Flora will be held September 13–15, 1990, at Mount Saint Vincent University, Halifax, Nova Scotia, Canada. The invited and contributing speakers will discuss the status and ecology of coastal plain communities and the protection and management of coastal plain habitat. This workshop will bring together scientific experts and representatives from conservation bodies and governments for round-table discussions to identify research and conservation actions and priorities. Opportunities to tour Nova Scotia's coastal plain will be provided. A proceedings will be published. For abstract submission forms and further information, contact:

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THE NEW ENGLAND BOTANICAL CLUB
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RHODORA July 1990 Vol. 92, No. 871

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# Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB

Vol. 92 October 1990 No. 872

# The New England Botanical Club, Inc.

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**Cover Illustration**

*Sabatia kennedyana* Fern. (Plymouth Gentian). A globally rare, disjunct species of the coastal plain of North America, occurring in northeastern South Carolina, southeastern North Carolina, southeastern New England, and Yarmouth County, Nova Scotia. Original artwork by Tess Feltes; from *New England's Rare, Threatened and Endangered Plants*. Crow, G. E. 1982. Reproduced by permission.

Rhodora

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NEW ENGLAND BOTANICAL CLUB

Vol. 92 October 1990 No. 872

RHODORA, Vol. 92, No. 872, pp. 213–231, 1990

# A NEW *SPIRANTHES* (ORCHIDACEAE) FROM THE CIENEGAS OF SOUTHERNMOST ARIZONA[1]

CHARLES J. SHEVIAK

## ABSTRACT

*Spiranthes* from isolated wetlands in Santa Cruz and adjacent Cochise Counties, Arizona, which in the past have been cited as *S. graminea* Lindl., differ from that species in several floral and vegetative characters and in chromosome number; they are readily separated from it by their few-septate trichomes. The more northern *S. diluvialis* Sheviak is larger-flowered with more ringent flowers and different flower and sepal orientation. The morphological and cytological features of the Arizona plants indicate that they represent a distinct species, described here as *S. delitescens* Sheviak. The cytology of this species suggests an origin through hybridization and amphiploidy, but the parental species are not identified.

Key Words: *Spiranthes delitescens, Spiranthes graminea, Spiranthes diluvialis,* Cienegas, Arizona

## INTRODUCTION

Scattered in the desert grassland of southernmost Arizona are isolated, usually spring-fed wetlands known as cienegas. At one such site northwest of Canelo, Santa Cruz County, P. S. Martin in 1968 discovered a population of *Spiranthes.* These orchids were subsequently determined by Luer as *S. graminea* Lindl. and were the basis for his inclusion of this otherwise Mexican species in the orchid flora of the United States (Luer, 1975). Subsequently, populations of comparable plants have been found at two other sites in Santa Cruz County and one in adjacent Cochise County.

While working on the identity of *Spiranthes diluvialis* Sheviak (Sheviak, 1984), I examined specimens and photographs of the Arizona plants referred to *S. graminea* and found them to differ

[1] Contribution #641 of the New York State Science Service.



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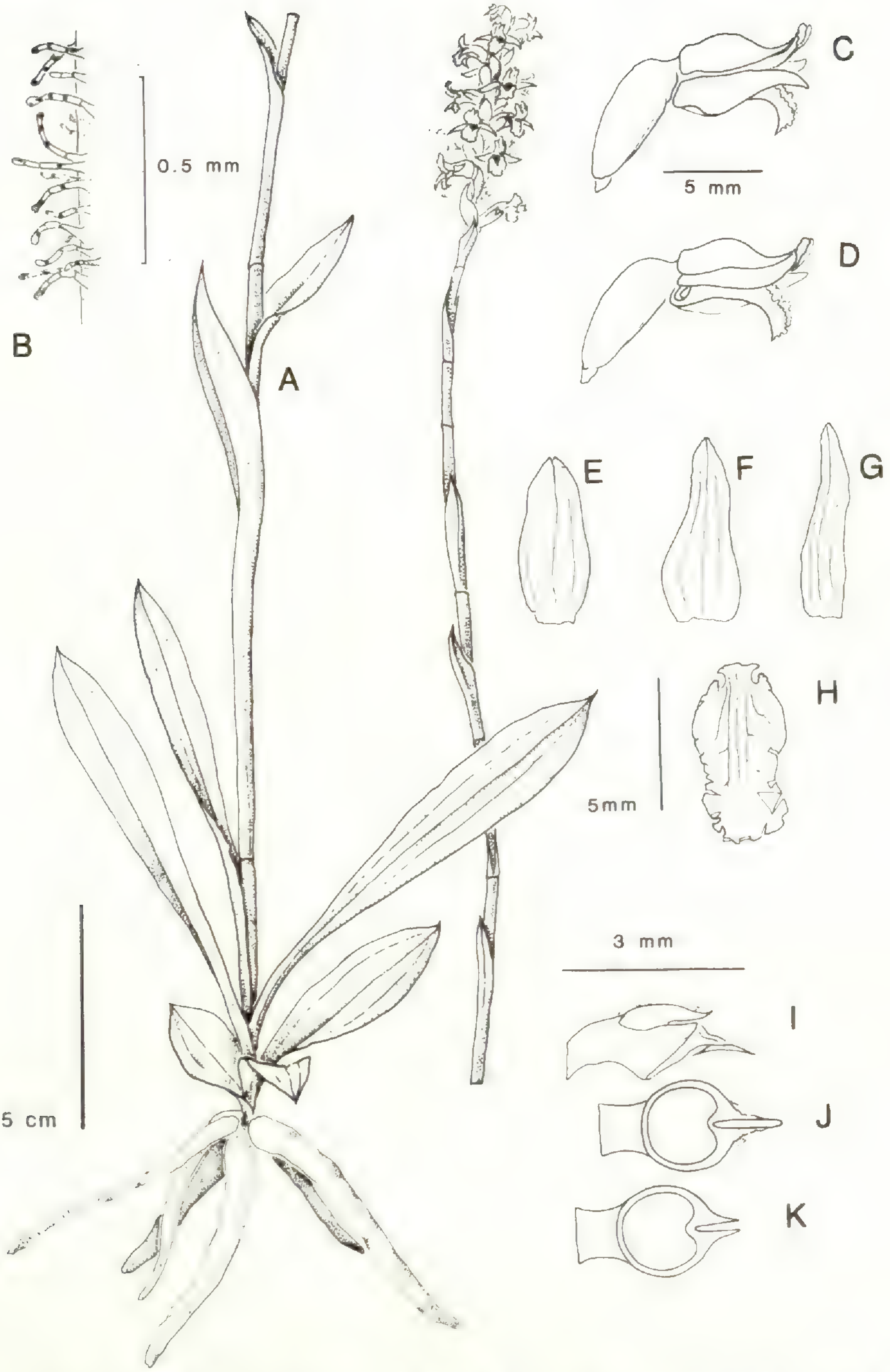


Figure 1. *Spiranthes delitescens* Sheviak. Drawings based on live plants *in hort.* and preserved specimens derived from *Burling s.n.* '*a*.' **A.** Habit. **B.** Portion of rachis showing trichomes. **C–K.** Camera lucida drawings from liquid-preserved flowers. **C.** Flower, lateral view. **D.** Flower, lateral view, lateral sepal removed.

from Mexican *S. graminea* and to resemble in some features the more northern plants subsequently described as *S. diluvialis.* A live Arizona plant collected for me in 1982 by M. A. Burling (*Burling s.n.,* NYS) bloomed the following year and provided material for morphological and cytological study. Preliminary results indicated that further study was warranted, and in 1984 I studied three of the known populations in the field. Collections from two of these (*Sheviak & Burling 2622, 2626*: NYS), including four live plants, provided additional material for comparison with *S. diluvialis* and *S. graminea.*

An important factor which initially hindered resolution of the problem was our poor state of knowledge concerning *Spiranthes graminea.* From study of specimens and photographs of Mexican plants, it appeared that two entities were included under this name. This situation made comparisons of Arizona and Mexican material difficult. Recently, the problem in Mexico was resolved by Catling and Catling (1988), and their work leading to the recognition of *S. nebulorum* Catling & Catling has provided much of the information necessary to resolve the present problem. Simultaneously, a live plant of *S. graminea* from the State of Mexico (*Kasselmann 56*) was provided by H. W. E. van Bruggen and fixed flowers of *S. nebulorum* (*Greenwood G-885*) were provided by E. W. Greenwood.

Through study of herbarium specimens and of live plants both in the field and under cultivation, the Arizona plants have been found to display a distinct set of morphological and cytological characteristics that clearly distinguishes them from their relatives. Hence, they represent a distinct species:

**Spiranthes delitescens** Sheviak, *sp. nov.* (Figure 1)

Herba erecta gracilis, persaepe 240–475 mm alta, inferne glabra, superne pubescens. Trichomata 2–5 septata, plerumque apicem versus angustata, capitata pro parte maxima capitulis diametro stipites aequantibus, ecapitata saepe acicularia. Radices tuberoso-incrassatae. Folia lineari-lanceolata vel oblanceolata, radicalia et in caule gradatim bracteis sursum reposita, sub anthesi persis-

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←

**E.** Dorsal sepal. **F.** Lateral sepal. **G.** Petal. **H.** Lip. **I.** Column, lateral view. **J.** Column, ventral view. **K.** Column, ventral view, pollinarium removed.

tentia. Spica persaepe 20–70 mm longa, 13–18 mm diametro. Perianthium 6.5–8.0 (–9.9) mm longum, album. Sepala plerumque ad basim connata, lateralia patenti-arcuascentia necnon plerumque descendentia. Labellum 5.8–7.9 mm longum, oblongum, infra laeve vel obscure verrucosum.

Herb, erect, slender, 240–475 mm tall (rarely shorter), glabrous below, pubescent above. Trichomes 2- to 5-septate, usually tapered toward the apex, of two types, non-capitate ones often acicular, capitate ones with glands mostly about the same diameter as their stipes. Roots tuberously thickened, about 5 mm in diameter. Leaves persisting past anthesis, linear-lanceolate to oblanceolate, the larger to 180 mm long and 15 mm wide (rarely wider), basal and cauline, the latter 5–10 in number and only gradually reduced upward to sheathing bracts 9–17 mm long, the lower half of the stem consequently leafy. Spike rather open to dense, with three flowers per cycle, 20–70 mm long (rarely longer), 13–18 mm in diameter. Floral bracts acuminate to attenuate, the lowermost 8–13 mm long. Flowers tubular, abaxially curved, becoming open with wide-spreading lateral sepals, perianth 6.5–8.0 (–9.9) mm long, white with the center of the lip creamy or very pale yellow. Sepals usually connate basally (the connation below the lip averaging 1.1 mm, up to 2.5 mm but sometimes absent), lanceolate, acute, the lateral curving outward throughout their lengths and usually directed somewhat downward, their apices wide-spreading. Petals for most of their lengths associated with the dorsal sepal, linear to linear-oblanceolate, obtuse, the apices spreading. Lip 5.8–7.9 mm long, oblong, the apex broadly expanded with extensive transverse pleats, smooth to obscurely verrucose below; basal calli stout, .4–1.4 mm long. Column slender; rostellum elongate, deeply bifid.

Chromosome number: $2n = 74$.

TYPE: U.S.A.: Arizona: Santa Cruz Co.: Marshy meadow, seeps, and hummocks in stream, along Turkey Creek, .5 mi. N of Canelo, SE¼ Sec 4, T22S, R18E. elev. 4035 ft. 1 August 1984. *C. J. Sheviak & M. A. Burling 2626* (HOLOTYPE: NYS).

PARATYPES. U.S.A.: Arizona: Cochise Co.: Babocomari Ranch, Babocomari Cienega above the dam. Along old railroad bed in marshy areas. elev. 4600 ft. 25 July 1981. *R. Bailowitz s.n.* (ARIZ); Santa Cruz Co.: O'Donnell Cienega, Knipe Ranch near Canelo, Sec 32 & 33, T21S, R18E. elev. 4950 ft. 7 July 1968. *P. S.*

*Martin s.n.* (ARIZ); Same locality, 10 July 1968. *P. S. Martin s.n.* (ARIZ); Same locality, 27 August 1969. *P. S. Martin s.n.* (ARIZ); Growing in seep on lower half of slope about 20 ft. south of main spring in bottom of drainage. Sheehy Spring, elev. 4700 ft. Greene (Sharpe) Ranch, San Rafael de la Zanja Grant, San Rafael Valley. 26 July 1980. *L. J. Toolin & F. W. Reichenbacher 936* (ARIZ); Seeping slope, S side of large Scirpus-dominated springy meadow. Sheehy Spring, Sharpe [Greene] Ranch, San Rafael de la Zanja Grant, 3 mi. NE of Lochiel, elev. 4700 ft. 1 August 1984. *C. J. Sheviak & M. A. Burling 2622* (NYS); Plants 'a' & 'b' from *C. J. Sheviak & M. A. Burling 2622, in hort.* 1985. *C. J. Sheviak 2750* (NYS); Wet boggy area just N of small pond. Most growing in moist grass with no standing water or on grassy hummocks surrounded by water. Turkey Creek, Canelo Hills. Cienega immediately N of AZ Hwy 83 crossing, Coronado National Forest, SE¼ SE¼ Sec 4 T22S, R18E, elev. 4963 ft. 29 July 1982. *F. Reichenbacher 1374* (ARIZ); Permanently marshy, hummocky meadow along east side of Turkey Creek ca. ¼ mi. N of Canelo, Sec 3–4 line, T22S, R18E. 30 July 1982. *M. A. Burling s.n.* (NYS); Same plant as *Burling s.n., in hort.* 1984. *C. J. Sheviak 2667* (NYS); Same plant as *Burling s.n., in hort.* 1985. *C. J. Sheviak 2749* (NYS).

ETYMOLOGY. Present participle of *delitescere,* to hide away, to hide one's self, in allusion to the species' isolated and long-unsuspected occurrence.

*Spiranthes delitescens* is distinguished by medium-sized flowers of a distinctive shape that is not seen in similar, possibly closely related, species. The flower is characterized by a pronounced ventrally-directed curve such that, in lateral view, the base appears ascending but the apex is horizontal or somewhat nodding. The aspect is of a curved tube. This is in contrast to the ascending flowers of *S. diluvialis* and the horizontal to nodding flowers of *S. graminea* and *S. nebulorum.* Flowers of both *S. diluvialis* and *S. graminea* are relatively slender and ringent; those of *S. delitescens* comparatively short and broad-based; in this respect they are perhaps more like those of *S. nebulorum.* The lateral sepals in *S. delitescens* differ in orientation from these other species: they curve uniformly outward and slightly downward such that the apices approach positions perpendicular to the axis of the flower. In contrast, the basal half of the lateral sepals in the other species are relatively straight: the variably directed sepals of *S. diluvialis* may spread laterally, but they do so from the very base; the apical third may then curve inward or outward. Similarly, in *S. graminea* sepals may be directed outward or outward and upward, but the apices converge above the rest of the flower. In some respects these features of *S. delitescens* are suggestive of *S. porrifolia* Lindl., with its ventrally curved flowers and lateral se-

pals widely outward-curving toward their apices. In other respects, however, *S. porrifolia* is a very different plant with very slender, yellowish flowers with lateral sepals appressed through most of their lengths and lanceolate to lance-ovate, acute lips (*see illustrations* Luer, 1975 and Sheviak, 1989).

The pubescence of *Spiranthes delitescens* is unusual and possibly unique. Glandular-capitate and eglandular trichomes are abundant on the rachis, in common with many species in the genus. In other glandularly pubescent species, however, individual trichomes, whether glandular or eglandular, are of essentially uniform thickness; the glands are notably broader than the stipes, resulting in a distinctly capitate pubescence. In *S. delitescens,* however, trichomes commonly taper toward the apices. Glands are for the most part about the same diameter as their stipes or may be even narrower, and non-glandular trichomes are commonly acicular. In this feature *S. delitescens* suggests *S. vernalis* Engelm. & Gray, which is characterized by acicular trichomes wholly lacking glands.

Many of the other characteristics of *S. delitescens* are those of either *S. graminea* or *S. diluvialis.* Its habit suggests the former: tall and slender with a disproportionately short inflorescence of small flowers, these densely arranged but sometimes disposed in an evident spiral about the rachis. These features are very clearly illustrated in the photographs published by Luer (1975). Leaves are typically much broader than in *S. graminea* and are more typical of *S. diluvialis,* but sometimes even wider than in that species. Roots are tuberous, as in *S. diluvialis,* not slender, widespreading, and stoloniferously producing shoots at the apices, as in *S. graminea.* All three species are characterized by pubescent inflorescences. As in most members of the genus, the multicellular, uniseriate trichomes of *S. delitescens* and *S. diluvialis* are composed of but a few cells and hence only 1–5 (usually 2–3, but occasionally –7 in *S. diluvialis*) septate. In contrast, *S. graminea* is remarkable in its very long, 8–11 septate trichomes, a characteristic shared with *S. nebulorum* (Catling and Catling, 1988); this characteristic alone serves to separate clearly *S. delitescens* from these two species. Trichomes of *S. graminea* are furthermore evidently nonglandular (P. M. Catling, pers. comm.) and noncapitate (at least predominantly so), in contrast to the glandularity of the other species. Flowers of *S. delitescens* are markedly smaller than those of *S. diluvialis,* although some overlap occurs, pri-

marily between those of a single known plant of *S. delitescens* with unusually large flowers (*Sheviak & Burling 2622a*) and some depauperate individuals of *S. diluvialis.* Sepals of *S. delitescens* are usually connate at the base to form a short tube (this most evident below the lip); this tube is usually also present in *S. diluvialis,* but in the specimens of *S. graminea* which I have seen, sepals are free to the base. The lip of *S. delitescens* strongly suggests that of *S. graminea*: oblong with a rather minor basal dilation and broad apex sometimes broader than the base, often with extensive transverse pleating of the apical portion. Lip shape in *S. diluvialis* is notably variable, but is characterized by a pronounced basal dilation wider to much wider than the apex. Lip venation is similar in all these species, the nerves relatively few, the laterals with widely diverging branches. The column of *S. delitescens* is slender, suggesting the proportions seen in *S. graminea* and in contrast to the stout columns of *S. diluvialis* and *S. nebulorum.*

## CYTOLOGY

Cytology provides a significant background for analysis of the pattern of morphological variation among these species and is important to an assessment of the status of *Spiranthes delitescens.*

Two distinct cytological series of species are known in the genus: a larger group with chromosome numbers based on 15, and a smaller group with numbers based on 22. The latter group includes *Spiranthes romanzoffiana* Cham. and *S. porrifolia,* important species in the West, whereas a few relictual populations of *S. magnicamporum* Sheviak mark the only known occurrence of members of the 15-based series in western North America (Sheviak, 1982, 1984, 1989).

In the present case, numbers were determined or were already known for all species except *Spiranthes nebulorum,* for which cytological material was not available. The single available plant of *S. graminea* (*Kasselmann 56*) yielded a count of $2n = 44$. The unusual situation in the amphiploid *S. diluvialis,* with $2n = 74$ and the formation of 37 bivalents, has already been described (Sheviak, 1984). Six plants of *S. delitescens* from two populations (*Sheviak & Burling 2622a, 2622b, 2622c, 2626a*; *Burling s.n., s.n.* '*a*') also were all found to be $2n = 74$ with the regular formation of 37 bivalents. Hence, like *S. diluvialis, S. delitescens* appears to

be an amphiploid derivative of hybridization between species belonging to the 15- and 22-based series.

## MORPHOLOGICAL ANALYSIS

The pattern of similarity in morphological characteristics among the species under consideration here probably reflects in part a shared genetic component of the 22-based cytological series. With the exception of *Spiranthes graminea* and *S. nebulorum,* between which a close relationship is indicated by their unusual pubescence, the morphological similarities in certain features among these species may be due more to group membership than to any specific relationship between species. As a group, the 22-based series exhibits three distinctive features: lips with only a few nerves, the lateral with widely diverging branches; lips varying in shape upon a general pattern of a dilated base and marked subapical constriction; and sepals variably connate at the base to form a short tube. The extreme expression of these conditions is found in the tubular, partially connate calyx and pandurate, typically three-nerved lip of *S. romanzoffiana*; in certain other species one or another of these features may be inconsistently present or wholly lacking.

The cytology of the group, even though incompletely known, imposes certain constraints on the interpretation of morphology and focuses efforts in particular directions. Clearly, despite similarities in habit, flower size, and lip shape, *Spiranthes delitescens* is distinct from *S. graminea.* This distinction is evident from cytology alone, but is supported further by vegetative and floral characters, especially pubescence, floral shape, and lateral sepal position. Although the cytology of *S. nebulorum* is unknown, its evidently close relationship to *S. graminea* and lack of significant characteristics in common with *S. delitescens* remove it from further consideration. In contrast to the other species in the group, the unusual cytology of both *Spiranthes diluvialis* and *S. delitescens* dictates that their relationship must be assessed in considerable detail.

### Cultivated Plants

Experience with plants grown indoors under controlled conditions has been useful in delimiting phenotypic variation and in

determining the potential expression of characters. As discussed previously, *Spiranthes* frequently exhibit great phenotypic plasticity. Plants found in a stressed condition in the field may be non-distinctive, often with smaller, rather generalized flowers, but when cultivated under more favorable conditions may produce larger flowers of more distinctive morphology (Sheviak, 1973, 1982, 1989). Even in vigorous plants, the flowers toward the apex of an inflorescence typically are smaller and distinctive features may be poorly expressed (Sheviak, 1982; Catling and Catling, 1988). In the present study, results with live plants addressed problems in interpretation of the evident differences between *S. delitescens* and *S. diluvialis,* and of variability within *S. delitescens* in habit and in shape and size of the flowers.

The habit with very tall, slender, and weak stem topped by a short inflorescence of relatively few flowers that is characteristic of *Spiranthes delitescens* could be a direct product of the plants' habitat. All four of the known stations for the species are dominated by dense sods of tall grasses and sedges. Clearly, the characteristic habit might reflect an etiolated condition. However, under cultivation, both indoors under high-intensity fluorescent light (sufficient to maintain normal habit in other *Spiranthes* grown with *S. delitescens,* including *S. diluvialis*) and outdoors in full sun, the characteristic habit developed.

The density of the inflorescence and the degree to which a single spiral of flowers (the parastichy) is evident varies within individuals. Plants that in the field displayed particularly open inflorescences, in subsequent years under cultivation have produced much denser inflorescences with three evident secondary ranks (orthostichies). Conversely, plants that have, over a period of years, typically produced dense inflorescences, in some cases have in one year developed an evident spiral.

Lateral sepal position and general floral shape vary with the age of the flower; development of the characteristic form illustrated in Figure 1 furthermore requires favorable conditions and may be suppressed in the field. Flowers figured by Luer (1975) are typical of early development; in time, and under appropriate conditions, the sepals spread more widely and the lip, petals, and dorsal sepal spread more fully, producing the broad-faced flower figured here.

Throughout the period of observation of cultivated *Spiranthes delitescens,* a few plants of *S. diluvialis* bloomed sporadically.

When well-grown the *S. diluvialis* were often substantially larger than most plants of that species found in the field, and even when depauperate they did not develop the habit nor the floral characters of *S. delitescens.*

## Statistical Analysis

The relatively large flowers of *2622a,* plasticity of some floral characters, and especially the paucity of specimens of *Spiranthes delitescens* available for study hampered interpretation. In an effort to determine the significance of perceived differences, a discriminant function analysis (DFA [SPSS PC+: Discriminant]) was performed on 53 specimens: 38 of *S. diluvialis* and 15 of *S. delitescens.* The latter sample includes all known specimens of quality sufficient for inclusion, and actually represents fewer individuals, as 4 of these specimens are cultivated samples of 3 of the field-collected plants included in the analysis. Specimens employed and their geographic origins are cited in Table 1.

Sixteen characters were measured; means, standard deviations, discriminant function character weights, and the order of correlation of characters within the function are presented in Table 2. Most of these characters are self-evident, but a few require clarification. Floral characters were measured in pressed flowers moistened in warm water. Ovary length is the distance from the point of attachment of the median nerve of the lateral sepal to the base of the ovary, which is evident as a dilation above the pedicel (if present). Floral tube maximum basal height measures, in the basal half of the perianth of flowers pressed laterally, the maximum distance from the median nerve of the dorsal sepal to the lower edges of the lateral sepals, the measurement made perpendicular to the axis of the flower. Lateral sepal connation is the length of the connate portion of the lateral sepals below the lip. Sepal separation is the distance separating the adjacent edges of the lateral and dorsal sepals, the measurement made perpendicular to the axis of the flower at its midpoint; positive values result from lateral sepals diverging downward from the dorsal, and negative from laterals rising upward and overlapping the dorsal. Callus length was obtained from the calli lying exclusively on one side of the lip (the right when viewing the inner (upper) surface of the lip with the base uppermost); this technique reduced the

Table 1. Specimens of *Spiranthes diluvialis* and *S. delitescens* employed in the Discriminant Function Analysis.

| Locality [County] | Collection | Specimen |
|---|---|---|
| *S. diluvialis* | | |
| Colorado | | |
| Jefferson | *Smookley s.n.* | COLO |
| | *Sheviak 2224* | NYS 'c' |
| | *Sheviak 2257* | NYS 'holotype,' 'a,' 'b,' '1' |
| | *Sheviak 2313* | NYS '1,' '2,' '3' |
| Nevada | | |
| Lincoln | *Hall s.n.* | BRY |
| Utah | | |
| Garfield | *Neese & White 3927* | BRY 'a,' 'b' |
| | *Sheviak 2300* | NYS 'a,' 'b,' 'c,' 'd,' 'e,' 'f,' '4,' '5,' '6' |
| Salt Lake | *Jones 1908* | MICH 'c'; MSC 'right' |
| | *Nielsen 221* | UT 'a,' 'b,' 'c,' 'd,' 'e' |
| Tooella | *Cottam 14361* | ARIZ 'b'; UT 'a,' 'b,' |
| Utah | *Barnett 154* | BRY 'a,' 'b' |
| Wayne | *Neese & White 3904* | BRY 'b,' 'c'; DAV 'a' |
| Weber | *Tracy 169/236* | MSC |
| | *Tracy & Evans 554* | NY 'a' |
| *S. delitescens* | | |
| Arizona | | |
| Cochise | *Bailowitz s.n.* | ARIZ 230519 |
| Santa Cruz | *Burling s.n.* | NYS |
| | *Martin s.n.* | ARIZ 167219'b' |
| | *Reichenbacher 1374* | ARIZ |
| | *Sheviak 2667* | NYS |
| | *Sheviak 2749* | NYS |
| | *Sheviak 2750* | NYS 'a,' 'b' |
| | *Sheviak & Burling 2622* | NYS 'a,' 'b,' '2' |
| | *Sheviak & Burling 2626* | NYS 'a,' '1' |
| | *Toolin & Reichenbacher 936* | ARIZ 'b' |

opportunity for bias arising from the often different lengths of the two calli on each lip.

Groups for the analysis were defined geographically: the more northern *Spiranthes diluvialis* from the Great Basin and the base of the Front Range in Colorado, and the plants from southernmost Arizona. Two distinct groups were recognized by DFA (Figure

Table 2. Means, standard deviations, discriminant function character weights, and order of correlation within the function for characters measured in the 53 specimens of *Spiranthes* cited in Table 1. Constant = 5.297525.

| Character | Means ($\sigma$) *S. diluvialis* | Means ($\sigma$) *S. delitescens* | Discriminant Function Character Weights (Correlation) | |
|---|---|---|---|---|
| BRACTS/LEAVES | | | | |
| Cauline: number | 6.0 (1.8) | 7.3 (1.7) | .2395277 | (9) |
| Cauline: length of uppermost | 20.2 (7.2) | 12.3 (2.4) | .1868922 | (5) |
| Floral: length of lowermost | 16.7 (5.2) | 10.5 (1.6) | −.3243319 | (4) |
| INFLORESCENCE | | | | |
| Length | 73.2 (28.7) | 52.4 (21.7) | .006118466 | (8) |
| OVARY | | | | |
| Length | 4.1 (1.2) | 4.0 (0.8) | .9171546 | (15) |
| Width | 3.0 (0.8) | 2.7 (0.5) | −.2975654 | (12) |
| FLORAL TUBE | | | | |
| Maximum basal height | 3.4 (0.6) | 3.2 (0.5) | .1886418 | (11) |
| SEPAL | | | | |
| Separation | −0.3 (0.6) | 0.3 (0.4) | .3421256 | (6) |
| Dorsal: length | 10.0 (1.5) | 7.2 (1.2) | .2877804 | (3) |
| Lateral: length | 10.5 (1.2) | 7.7 (0.8) | −.6379773 | (1) |
| Lateral: connation | 0.6 (0.6) | 1.1 (0.7) | 1.291342 | (7) |
| LIP | | | | |
| Length | 8.9 (1.0) | 6.8 (0.6) | −.7362284 | (2) |
| Maximum basal width | 4.4 (0.9) | 3.9 (0.5) | −.7828668 | (10) |
| Minimum median width | 2.4 (0.7) | 2.4 (0.4) | .6284711 | (16) |
| Maximum apical width | 3.2 (0.8) | 3.3 (0.6) | .1752346 | (14) |
| Callus length | 0.8 (0.3) | 0.9 (0.2) | .8802953 | (13) |

2), and these corresponded to the groups established geographically. No specimens were misclassified (assigned by geographic origin to one group but morphologically referable to the other).

## DISCUSSION

### Status of *Spiranthes delitescens*

The cytology of *Spiranthes delitescens* indicates an amphiploid origin involving hybridization of species from each of the two cytological series of the genus, those based on 15 and 22 chro-

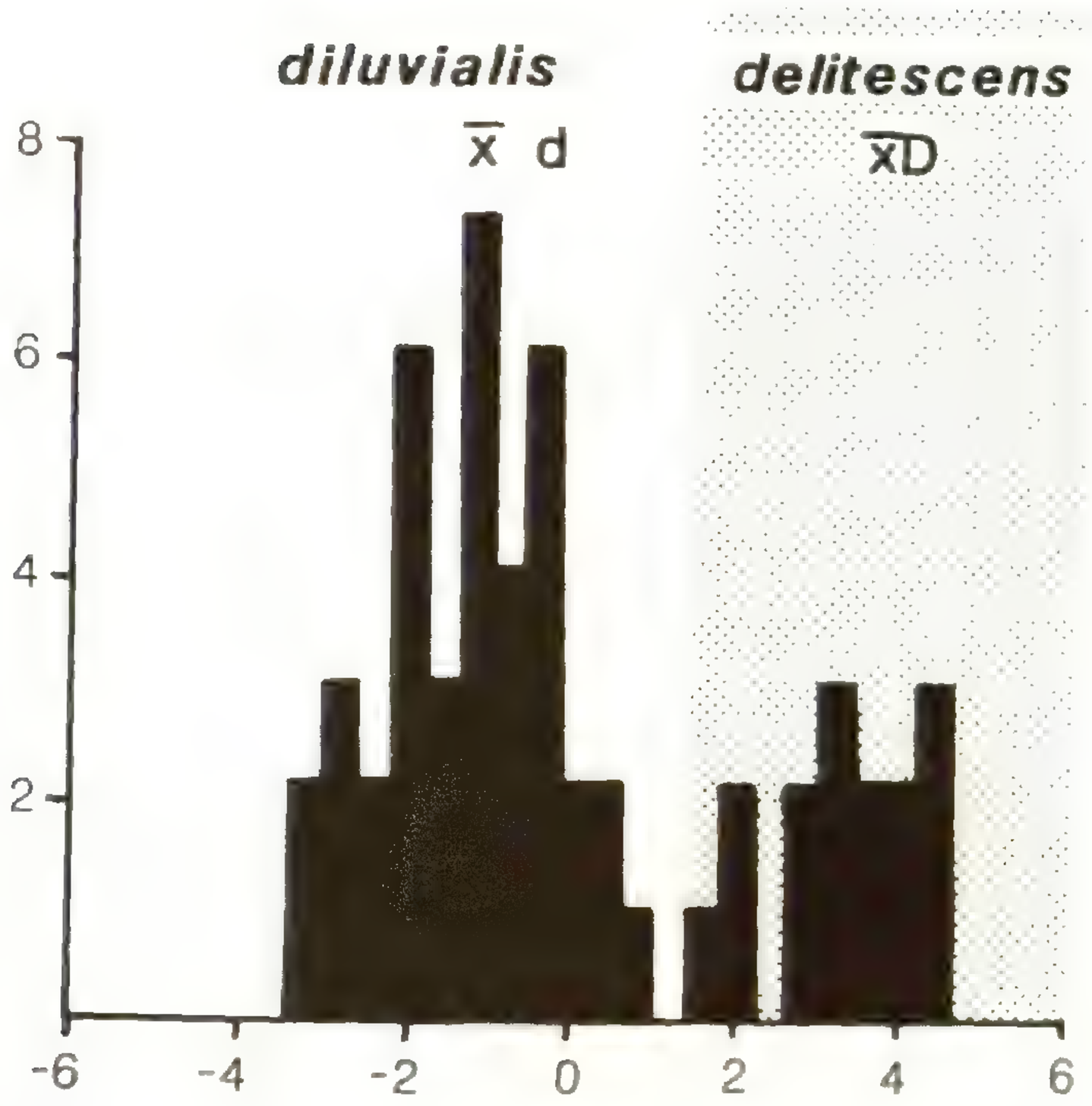


Figure 2. Discriminant scores of 38 specimens of *Spiranthes diluvialis* and 15 of *S. delitescens.* Also plotted are group centroids (x) and the holotypes of *S. diluvialis* (d) and *S. delitescens* (D).

mosomes. Such an origin is shared with *S. diluvialis.* The status of *S. delitescens* consequently depends on its relationship with this species. Do the two taxa have a common origin, are they the results of separate crosses between the same species, do they share a single parent, or are their similarities due to relationships between their parents? The morphological data are sufficient to demonstrate that *S. delitescens* arose independently from *S. diluvialis,* but an understanding of its origin is ellusive.

The results of DFA indicate that, indeed, *Spiranthes delitescens* is morphologically distinct from the more northern *S. diluvialis,* but these results are not necessarily inconsistent with an hypothesis of long isolation and drift of a limited gene pool. Perhaps *S. delitescens* merely represents the small end of a discontinuous range in size of various characters within *S. diluvialis* Most of the characters summarized in Table 2, including the five most strongly discriminating, show *S. diluvialis* to be the larger. Connation of the lateral sepals, however, is markedly greater in *S. delitescens,* despite the overall smaller flower size, and callus length also averages slightly greater in this species. The number

of cauline bracts and leaves is usually greater in *S. delitescens* than in the somewhat shorter *S. diluvialis*; this difference probably is not the result of a simple relationship between bract number and stem length, because a broader study of the *S. romanzoffiana* complex suggests that bract number may differ between taxa regardless of the stature or vigor of individuals or the conditions under which they may be growing.

The orientation of the lateral sepals of *Spiranthes delitescens* is unlike that of any otherwise similar species. This feature involves both the curving of the sepals and their position relative to the dorsal sepal. Similarly, the curve of the flower of *S. delitescens* as viewed from the side is not seen in *S. diluvialis.* The unusual pubescence of *S. delitescens* is particularly significant, because infraspecific variation sufficient to accommodate such trichomes within *S. diluvialis* is simply unknown in the genus. These unique features of *S. delitescens* are furthermore not those of either of the apparent parents of *S. diluvialis,* i.e., *S. romanzoffiana* and *S. magnicamporum.* Hence the origin of *S. delitescens* seems quite clearly to have been through hybridization of different species than was that of *S. diluvialis,* dictating that these two taxa be treated as distinct at the specific level.

*Spiranthes delitescens* is the third species of the genus to be described from the western United States in recent years. Along with a few disjunct occurrences of *S. magnicamporum* now known in the region and Catling and Catling's recent work in Central America, no available key adequately treats the genus in this geographic area. Accordingly, a key to the species in western North America and in Central America is included here. For Central American species it is based, largely verbatim, on the key of Catling and Catling (1988).

## KEY TO *SPIRANTHES* IN WESTERN NORTH AMERICA AND CENTRAL AMERICA

1. Rachis and upper portion of stem densely pubescent; the longest trichomes .4–.6 mm long, 8–11 septate; flowers relatively small, perianth 5–7 mm long. (Central America) . . 2
2. Lip oblong-ovate or oblong-quadrate, not strongly curving from the claw and the floral tube straight and not widened basally; basal calli .4–.8 mm long; lateral sepals 1.2–1.8 mm wide ..... *S. graminea* Lindl.

2. Lip broadly ovate, strongly curving upward from the claw and consequently the floral tube arched and widened basally; basal calli .9–1.8 mm long; lateral sepals 1.7–2.8 mm wide ..... *S. nebulorum* Catling & Catling

1. Rachis and upper portion of stem glabrous to densely pubescent, the trichomes 1–5 (rarely to 7) septate; flowers various, perianth 4–14 mm long ..... 3

3. Rachis and upper portion of stem densely pubescent, trichomes all non-capitate and tapering to often sharp-pointed apices; flowers in an evident, open spiral ..... ..... *S. vernalis* Engelm. & Gray

3. Rachis and upper portion of stem glabrous to rather densely pubescent, many of the trichomes glandular-capitate; flowers in an open to very tight spiral, the inflorescence then dense and the primary coil of flowers obscure ... 4

4. Glands of the capitate trichomes inconspicuous, mostly about the same diameter as the stipe or smaller; trichomes commonly tapered toward the apex, the non-capitate often acicular; lip oblong; lateral sepals arcuate spreading. (Southern Arizona) ..... ..... *S. delitescens* Sheviak

4. Glands of capitate trichomes conspicuous, markedly broader than the stipe; trichomes of uniform thickness below the gland, the non-capitate blunt or truncate; flowers various ..... 5

5. Flowers in a very open spiral with many more than 5 flowers per cycle ..... 6

6. Lip ovate or elliptical, center of lip green. (Central America) ... *S. tortile* (Thurm.) Garay & Sweet

6. Lip pandurate, white. (California & Oregon) ... ..... *S. romanzoffiana* Cham. (a local race, possibly a distinct taxon)

5. Flowers in an open to very tight spiral, 3 or 4 secondary ranks then evident, usually 3 and not more than 5 flowers per cycle ..... 7

7. Rachis glabrous or sparsely pubescent, the longest trichomes less than .18 mm long (usually much less), the glands often sessile or subsessile; sepals connate at the base ..... 8

8. Lip broadest at the base, membranaceous,

white or ochroleucous; perianth 8–12 mm long (rarely shorter) ..... 9

9. Lip pandurate, the apex dilated, glabrous above; sepals & petals united throughout their lengths and forming a hood ..... ..... *S. romanzoffiana* Cham.

9. Lip ovate to lanceolate, the apex only slightly or not at all dilated, with a dense cushion of peg-shaped trichomes above; sepals & petals with apices free & spreading ..... *S. porrifolia* Lindl.

8. Lip broadest near the middle; the base distinctly narrowed, thick and fleshy, green; perianth 4–6 mm long ..... ..... *S. infernalis* Sheviak

7. Rachis sparsely to densely pubescent, the longest trichomes .19 mm long or longer (often much longer; very rarely shorter, then the lip not pandurate and the sepals and petals not united nor forming a hood), the glands obviously stalked; sepals fused at the base or free ..... 10

10. Lip without a marked subapical constriction, calli short, conical; sepals free to the base; flowers nodding; leaves wholly basal, fugaceous, usually absent at anthesis ..... ..... *S. magnicamporum* Sheviak

10. Lip with a marked subapical constriction, the base usually dilated, calli often elongated; sepals often basally connate; flowers ascending; a few leaves on the base of the stem, persisting through anthesis ..... ..... *S. diluvialis* Sheviak

**Origin of *Spiranthes delitescens***

The distinctive features of *Spiranthes delitescens* include habit, pubescence, floral shape, sepal orientation and connation, and lip shape and venation. These should serve to indicate at least one of its parents, but the origin of the characteristics is unknown. Lip venation in *S. delitescens* is typical of the condition seen in all members of the 22-based series; lip shape, with minor sub-

apical constriction, may represent merely a suppression of this feature by the parent from the 15-based series. The general habit of *S. delitescens* suggests that of *S. graminea,* and the lips of these species are very similar. The free lateral sepals which I have seen in specimens of *S. graminea,* however, if typical, would seem to preclude the species as a parent, because of the marked sepal connation in *S. delitescens*: this feature must come from the 22-based parent. Floral shape and sepal orientation suggest *S. porrifolia,* with its narrowly curving flowers and lateral sepals curving outward toward the apices; this member of the 22-based series would seem to be a possible contributor of these features. The other parent in such a cross is not obvious. Indeed, of known extant western species, *S. graminea* and *S. porrifolia* would seem to provide the proper combination of salient features, but such a cross is not in keeping with the cytological evidence.

The pubescence of *S. delitescens* suggests ancestry involving *S. vernalis.* Significantly, an artificial hybrid of *S. vernalis* and *S. odorata* (Nutt.) Lindl. (*Sheviak 2569*) is densely pubescent with tapering trichomes, the capitate ones with reduced glands. The habit of this plant furthermore is very similar to that of *S. delitescens,* with long slender stem bearing leaves at the base and short, rather dense inflorescence with flowers smaller than those of either parent. Hence *S. vernalis* could indeed serve as a parent: the shape of its trichomes is conveyed, even affecting the size of the glands, which are thus suppressed but nonetheless present; the open spiral of its inflorescence is missing, and a habit suggesting that of *S. delitescens* is produced, even with the large, stout *S. odorata* as the other parent. The curved flowers of *S. delitescens* are not predictable products of a cross of *S. graminea* and *S. vernalis,* however. The tuberous roots of *S. delitescens* are likewise not to be expected, but this feature is not so pronounced as in some other species, and they are perhaps not unlike roots in some *S. vernalis.*

That an artificial hybrid employing *Spiranthes vernalis* and *S. odorata,* a plant without any particular similarity to *S. delitescens,* could in fact simulate this species in habit and pubescence suggests that *S. vernalis* might indeed be a parent, and that a cross with the tuberous-rooted *S. porrifolia* is a possibility. Such a cross might yield the appropriate floral shape and would be expected to produce suitably curved lateral sepals. Arguing against such an origin is the present wide separation of the ranges of these two

species. Although *S. vernalis* is widespread in the southern plains and may have occurred in the Southwest during the Pleistocene, as was apparently the case with *S. magnicamporum* (Sheviak, 1984), the current disjunct populations which support such an interpretation for the latter species are not known for *S. vernalis*.

Although the morphological evidence allows some speculation, the largely unknown genetics of the group, as emphasized by some of the characteristics of the artificial hybrid mentioned above, emphasizes the difficulty in identifying ancestral species. The origin of *S. delitescens* is thus obscure.

## A NOTE ON RARITY

I visited all of the four known stations for *Spiranthes delitescens* and located the plant at three (time at the fourth was inadequate to assess the status of the plant, but the habitat, at least, was intact). Martin's original discovery site was acquired by The Nature Conservancy and is managed as one of their preserves. The status of the species on the preserve is a prime focus of attention. The species is abundant at Sheehy Spring, but is very restricted within a larger area of seemingly suitable habitat. The population along Turkey Creek is the most extensive and may cover a greater area than the specimen data indicate. Although one expects the species to be found at additional sites in the future, the nature of its habitat severely limits the possibilities. It is almost certain that *S. delitescens* occurs in Mexico, perhaps widely so, but P. M. Catling reported (pers. comm.) that he had not encountered specimens during his work. Whatever its distribution in Mexico may prove to be, it is clear that *S. delitescens* is extremely rare and restricted in the United States.

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source of information and inspiration. I owe my field success in Arizona to the efforts of Mim Burling, McNeal, Arizona, whose initial reconnaissance of a number of possible sites facilitated a productive visit, and whose original collections were in large part responsible for the formalization of this study. For their provision of specimens, photographs, and first-hand information, I am indebted to Thomas Todsen, Las Cruces, New Mexico; Stephen Blecher, Littleton, Colorado; H. W. E. van Bruggen, Heemskerk, The Netherlands; Christel Kasselmann, Berlin; and E. W. Greenwood, Oaxaca. The critical drawings were prepared by P. McC. Kernan. Helpful criticisms of the manuscript were provided by P. M. Catling. This study was supported in part by grants from the Denver Botanic Gardens.

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# PHYTOGEOGRAPHY OF BERKSHIRE COUNTY, MASSACHUSETTS[1]

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## ABSTRACT

Origin of the present vegetation of Berkshire County, Massachusetts, is discussed, with emphasis on glaciation, refugia of floristic elements during glaciation, migration patterns of taxa, and the effect these factors may have had on the present composition of the flora. The vegetation can be divided into five affinity groups: Eastern Deciduous Forest Region including a Southern and Midwestern sub-group, Alleghanian (Glaciated northeast and Appalachian Mountains), Boreal, Coastal Plain and Alien. Many taxa in the county are at or near their northern, southern, or eastern range limits. Selected state-listed rare taxa and common species are used to illustrate possible patterns of migration and limitations of distribution.

Key Words: Plant geography, flora, affinities, rare plants, Berkshire County, Massachusetts

## I. FLORISTIC PROVINCE

Berkshire County lies within the Appalachian Province of the Atlantic North American Region as defined by Takhtajan (1986) and Cronquist (1982). This province corresponds generally to the area described by Braun (1950) as the Eastern Deciduous Forest and to the Eastern Deciduous Forest Province of Gleason and Cronquist (1964). The most widespread and characteristic type of vegetation is the deciduous forest which, in Berkshire County, includes such species as *Acer saccharum, A. rubrum, Fagus grandifolia, Quercus rubra, Q. alba, Betula papyrifera, B. lenta, B. alleghaniensis, Carya ovata, C. cordiformis, Tilia americana, Fraxinus americana, Prunus serotina, Juglans cinerea, Populus deltoides,* and *P. grandidentata.* Authorities of these and other species are given in Table 1. Important evergreen components of this Region are the conifers *Pinus strobus* and *Tsuga canadensis.* An abundant understory layer, an herbaceous ground cover, and, in favorable soils, a rich vernal flora are an integral part of the deciduous forest.

Since Berkshire County is situated in the northeastern section of the Appalachian Province, where it is relatively close to the

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[1] Scientific contribution no. 1654 from the New Hampshire Agricultural Experiment Station.

Table 1. Phytogeographic affinities of rare plants of Berkshire County. E = Endangered, T = Threatened, SC = Special Concern, H = Historical.

**Widespread.** Species follow approximately the boundaries of the Eastern Deciduous Forest.

*Ophioglossum vulgatum* L. T
*Sagittaria cuneata* Sheldon T
*Eragrostis frankii* C. A. Meyer SC
*Panicum gattingeri* Nash SC
*P. philadelphicum* Bernh. SC
*Sphenopholis nitida* (Biehler) Scribn. T
*Carex hitchcockiana* Dewey SC
*C. sterilis* Willd. T
*C. typhina* Michx. T
*Eleocharis intermedia* (Muhl.) Schultes T
*Scirpus pendulus* Muhl. SC
*Corallorhiza odontorhiza* (Willd.) Nutt. E
*Morus rubra* L. E
*Claytonia virginica* L. T
*Waldsteinia fragarioides* (Michx.) Tratt. SC
*Linum medium* (Planch.) Britt. T
*Acer nigrum* Michx. SC
*Hypericum ascyron* L. (*H. pyramidatum* Ait.) T (H in county)
*Panax quinquefolius* L. SC
*Sanicula gregaria* Bickn. T
*Gentiana andrewsii* Griseb. T
*Verbena simplex* Lehm. E
*Blephilia ciliata* (L.) Benth. E
*B. hirsuta* (Pursh) Benth. E
*Veronicastrum virginicum* (L.) Farw. SC
*Hedyotis longifolia* (Gaertn.) Hook. (*Houstonia longifolia* Gaertn.) T
*Symphoricarpos albus* var. *albus* (L.) Blake (H in county)
*Lobelia siphilitica* L. T

**Southern and midwestern.** Species centered to the south and midwest and are at or near their northern or eastern limits in the county.

*Lygodium palmatum* (Bernh.) Sw. SC (H in county)
*Asplenium montanum* Willd. E
*A. ruta-muraria* L. T
*Elymus villosus* Muhl. T
*Carex alopecoidea* Tuckerm. E
*C. bushii* Mack. E
*C. davisii* Schw. & Torr. E
*C. formosa* Dewey E
*C. grayi* Carey T
*C. schweinitzii* Dewey E
*C. tetanica* Schkuhr T
*C. trichocarpa* Muhl. T
*Arisaema dracontium* (L.) Schott T

Table 1. Continued.

*Chamaelirium luteum* (L.) Gray E
*Quercus macrocarpa* Michx. SC
*Q. muhlenbergii* Engelm. SC
*Minuartia michauxii* (Fern.) Farw. (*Arenaria stricta* Michx.) SC
*Cimicifuga racemosa* (L.) Nutt. E
*Hydrastis canadensis* L. E
*Cardamine douglassii* (Torr.) Britt. E
*Agrimonia pubescens* Wallr. T
*Ilex montana* Torr. & Gray T
*Hydrophyllum canadense* L. E
*Trichostema brachiatum* L. T
*Veronica catenata* Pennell E
*Lonicera hirsuta* Eat. E
*Viburnum rafinesquianum* Schultes T
*Aster prenanthoides* Muhl. T

**Alleghanian.** Species centered in glaciated district with extension south in Appalachian Mountains.

*Thuja occidentalis* L. E
*Milium effusum* L. T
*Potamogeton hillii* Morong SC
*Sporobolus neglectus* Nash E
*Carex baileyi* Britt. E
*Rhynchospora capillacea* Torr. E
*Sisyrinchium mucronatum* Michx. T
*Arethusa bulbosa* L. T (H in county)
*Cypripedium calceolus* L. var. *parviflorum* (Salisb.) Fern. E
*Cypripedium reginae* Walt. SC
*Platanthera flava* (L.) Lindl. var. *herbiola* (R. Br.) Luer T (H in county)
*Clematis occidentalis* (Hornem.) DC. SC
*Adlumia fungosa* (Ait.) Greene T
*Arabis lyrata* L. T
*Amelanchier sanguinea* (Pursh) DC. SC
*Rhododendron maximum* L. T
*Calystegia spithamaea* (L.) Pursh (*Convolvulus spithamaeus* L.) (H in county)

**Boreal, including Circumpolar.** Species that have a center in the Canadian Biome.

*Equisetum scirpoides* Michx. SC
*Lycopodium selago* L. E (H in county)
*Cryptogramma stelleri* (Gmel.) Prantl T
*Polystichum braunii* (Spenner) Fee E
*Woodsia glabella* R. Br. E
*Sparganium minimum* (Hartm.) Fries E
*Potamogeton friesii* Rupr. E
*Trisetum triflorum* (Bigelow) Löve & Löve ssp. *molle* (Michx.) Löve & Löve E
*Carex castanea* Wahlenb. E
*C. lenticularis* Michx. T
*C. michauxiana* Boeck. E

Table 1. Continued.

*C. pauciflora* Lightf. E
*Eriophorum gracile* W. D. J. Koch T
*Juncus filiformis* L. T
*Luzula parviflora* (Ehrh.) Desv. ssp. *melanocarpa* (Michx.) Hamet-Ahti E
*Cypripedium arietinum* R. Br. E (H in county)
*Goodyera repens* (L.) R. Br. E
*Malaxis brachypoda* (Gray) Fern. T
*Platanthera dilatata* (Pursh) Lindl. T
*Salix serissima* (Bailey) Fern. SC
*Alnus viridis* (Chaix.) DC. ssp. *crispa* (Ait.) Turrill SC
*Betula pumila* L. T
*Arceuthobium pusillum* Peck SC
*Moehringia macrophylla* (Hook.) Fenzl E
*Nuphar pumila* (Timm) DC. (*N. luteum* [L.] Sibthorp & Sm. ssp. *pumilum* [Timm] E. O. Beal) T (H in county)
*Ranunculus pensylvanicus* L.f. T
*Cardamine pratensis* L. var. *palustris* Wimm. & Grab. (*C. pratensis* L.) T
*Ribes lacustre* (Pers.) Poir. SC
*R. triste* Pallas SC
*Amelanchier bartramiana* (Tausch) Roemer T
*Rosa acicularis* Lindl. E
*Sorbus decora* (Sarg.) Schneider E
*Viola nephrophylla* Greene T
*Conioselenium chinense* (L.) BSP. SC
*Pyrola asarifolia* Michx. var. *purpurea* (Bunge) Fern. E
*Vaccinium vitis-idaea* L. ssp. *minus* (Loddiges) Hultén E
*Stachys palustris* L. T
*Galium labradoricum* (Wieg.) Wieg. SC
*Petasites frigidus* (L.) Fries var. *palmatus* (Ait.) Cronq. T
*Solidago macrophylla* Pursh SC
*S. glutinosa* Nutt. ssp. *randii* (Porter) Cronq. (*S. spathulata* DC. ssp. *randii* [Porter] Cronq.) E

**Coastal Plain and eastern.** Species that are centered to the east.

*Carex polymorpha* Muhl. E (H in county)
*Orontium aquaticum* L. T

Atlantic-Gulf Coastal Plain Province and in close proximity to the Canadian Province (Takhtajan, 1986), it is not surprising that it contains phytogeographic elements of both these provinces. Sufficiently high mountains (up to 1064 m) in the northern part of the county provide climatic conditions that allow a southerly extension of species of the Canadian Province. Sandy outwash plains and acid, boggy marshes provide conditions suitable for a few Coastal Plain species.

One of the most interesting aspects of the Appalachian Province is the great number of taxa that are very similar to those of the Eastern Asian region. The following genera, which are found in Berkshire County, occur only in eastern United States and in eastern Asia (Li, 1952): *Camptosorus, Carya, Caulophyllum, Hydrastis, Liriodendron, Penthorum, Hamamelis, Parthenocissus, Panax, Aralia, Nyssa,* and *Epigaea.* Most of these genera, except for *Carya,* consist of one species in eastern United States and several in eastern Asia. In addition, vicariads that share this east-west distribution occur in many other more widespread genera.

## II. MAJOR FOREST COMMUNITIES

The Southern Appalachians form the center of highest diversity of the Eastern Deciduous Forest (Gleason and Cronquist, 1964). As distance increases from this center, the number of species decreases. The relative abundances of species in different regions vary widely, leading to the development of a number of plant associations or communities within this great biome. Seldom does any vegetational grouping have discrete boundaries, however, except in extremes of soil or microclimatic changes. There are usually transition zones in the area where two associations are contiguous (Gleason and Cronquist, 1964).

Küchler (1964) mapped plant communities for the vegetation of the United States and based his classification on the dominant species. He also characterized them by species usually found associated with that community. Four communities are mapped for Berkshire County: Northeastern Spruce-Fir Forest (*Picea-Abies*), Northern Hardwoods-Spruce Forest (*Acer-Betula-Fagus-Picea-Tsuga*), Northern Hardwoods Forest (*Acer-Betula-Fagus-Tsuga*) and an area that Küchler designated as Transition Zone between Appalachian Oak Forest (*Quercus*) and Northern Hardwoods Forest (cf. "Transition Hardwoods" of Westveld, 1956). This classification recognizes the wide variation that occurs in the county from north to south and from high to low elevations.

In reality, given the diversity of bedrock, elevation, slope, soil and water regimes, these zones or communities may be found as a mosaic within a small area, along with transition zones, making it difficult at times to discern an area on the ground that corresponds exactly to any one zone. Because of the extremes of elevation encountered in the northern part of the county (1064 m

to 175 m), one could map, along a transect 6 miles long, Spruce-Fir Forest and Appalachian Oak Forest, complete with *Cornus florida, Sassafras albidum* and dwarfed *Pinus rigida,* noting also, in between these extremes, the other communities as well.

Spruce-Fir Forest is found on the highest elevations in the north, from about 800 m to 1064 m. Northern Hardwood-Spruce Forest best characterizes the Berkshire Plateau (Egler, 1940), which extends along the eastern boundary of the county. Northern Hardwood Forest is perhaps the most widespread type, especially in the northern half where it is found on mid- to lower slopes and valley floors. *Quercus rubra* often is an important tree in this forest. Various types of oak forest intermix with northern hardwoods, depending on slope and soil. Toward the southern part of the county, *Pinus strobus, P. rigida, Tsuga canadensis, Quercus* spp., and *Carya* spp. become much more common as part of Küchler's Transition Zone.

Although the county is a comparatively small area, it contains a great diversity of species; factors that control or determine the limits of a species are complex. Stebbins (1980) proposed at least three such factors: genetic makeup, the environment in which the species grows, and past history of the population. It is the past history of the present vegetation, including the effects of various climatic changes and migration patterns, which is the main concern here.

## III. GLACIATION AND ITS EFFECT ON VEGETATION

The greatest single factor that has determined the composition of our flora is glaciation. Glacial periods resulted in elimination or displacement of the widespread, more homogeneous, deciduous and sub-tropical flora of the Northern Hemisphere and a subsequent mixing of both northern and southern elements (Wood, 1970).

During the middle Tertiary period, at least 50 million yr. B.P. (before present), before the series of glaciations began to spread over the northern portions of the earth, a broad band of vegetation known as the Arcto-Tertiary Flora covered the Circumpolar region (Chaney, 1947). This forest contained many genera of our present deciduous forest and ranged approximately 20 degrees farther north of its present range (Larsen, 1980). Wolfe (1978)

postulated that a tropical broad-leaved evergreen forest existed along the Pacific Coast in Washington from 50–34 million yr. B.P., indicating that the Arcto-Tertiary Flora was not purely deciduous or as homogeneous as once was thought. The Brandon Lignite, a Tertiary deposit dating from 32–34 million yr. B.P. (Oligocene) found in north-central Vermont, has yielded megafossils that indicate that the flora was most similar to modern floras of southeastern United States and southeastern Asia. The two species that Tiffney described, *Illicium avitum* (Tiffney and Barghoorn, 1979) and *Turpinia uliginosa* (Tiffney, 1979), belong to genera that presently inhabit warm-temperate, subtropical and tropical areas. Many species now restricted in range, such as *Liriodendron* and *Nyssa,* were widespread in the Tertiary (Wood, 1970). Herbaceous plants are not well represented in the sparse fossil record, so their presence as part of the Tertiary Flora is inferred from their existence in our own floristic assemblage (Wood, 1970).

A cooling trend in the late Tertiary, 27–2.5 million yr. B.P., resulted in a temperate deciduous forest that supplanted the warm-temperate forest at higher latitudes (Larsen, 1980), which was rapidly replaced by Arctic and Boreal species now found in the North. This cooling trend culminated in the formation of persistent ice in Polar regions.

The Quaternary Period, beginning 2.5 million yr. B.P., saw the extensions of these glaciers southward over portions of the landmasses of North America, Europe and Asia. There have been up to 18–20 glacial advances of approximately 100,000 years duration (Davis, 1983), interspersed with short interglacial warm periods of 10,000–15,000 years duration. Vegetation was repeatedly forced to migrate south during the long cold periods, which occupied 90% of the Quaternary. During the short warming intervals, the vegetation again migrated north. Climatic changes during the short interglacial periods were fairly abrupt (Davis, 1983). This oscillation resulted in much vegetational instability. Recent work based on pollen records has established that plant species migrated individually, not as plant communities (Davis, 1983; Wood, 1970). According to Davis (1983), communities formed south of the glacial border were made up of assemblages not seen today.

There are differing views as to the extent of vegetational change in unglaciated regions. Braun (1947, 1950, 1955) suggested that

the deciduous forest retreated from higher elevations and was infiltrated by boreal species; additionally, boreal species reached southward along the mountain ridges. Braun suggested that a narrow band of tundra may have existed near the glacier, but the eastern deciduous forest retained its identity and most of its extent. The fact that the rather specific habitat requirements of some presently rare herbaceous species would make migration difficult was used by Braun (1955) to indicate that the deciduous forest could not have been totally displaced during the Wisconsin glaciation. Other authors (Davis, 1983; Jacobson et al., 1987) postulated that wide bands of tundra and boreal forest reached far into the south, and that most deciduous species were dispersed into scattered refugia. This viewpoint was based on extensive pollen records, but as Larsen (1980) stated, these records tell only part of the story because many species do not shed large amounts of pollen, and positive identification of species is sometimes impossible.

Using pollen profiles from bogs and ponds throughout the eastern half of North America and sediments that have been radiocarbon-dated, Davis (1983) mapped full-glacial floras and traced the return northward of some of our more important trees. Since pollen grains are produced in different amounts by different species and may be transported varying distances, the precise composition of the flora cannot be defined, but fossil pollen profiles have been compared to modern ones from various vegetational types to check their accuracy. Davis and Goodlett (1960), in a study of modern pollen deposition in Vermont, found that several tree species are over-represented, such as oak (*Quercus*), pine (*Pinus*) and birch (*Betula*). Tree species that are under-represented are maple (*Acer*), arbor-vitae (*Thuja*), fir (*Abies*), poplar (*Populus*), larch (*Larix*), and basswood (*Tilia*). Davis (1983) also stated that it is still unclear where many deciduous species survived. Given these cautions, the refugia and migration routes northward of a few of our species can be postulated.

Coniferous pollen seems to dominate the unglaciated region at full-glacial time, but fossil seeds and fruits of some deciduous species have been found near Memphis, Tennessee (Davis, 1983). *Quercus* and *Carya* were prevalent in northern Florida. Davis suggested that populations of deciduous trees may have survived in small, scattered, unusual habitats that served as refugia. Wolfe (1951) postulated similarly that sheltered, cave-like grottoes, be-

cause of their more equable climate, may have served as refugia for certain species of restricted habitat close to the glacial margin.

According to Davis (1983), spruce (*Picea* spp.) migrated north from a widespread distribution in the south into the Appalachian Mountains and northeastward into New England. Larch (*Larix laricina*) persisted only on the eastern edge of the Great Plains and moved northeast from west of the Appalachians. The jack/red pine (*Pinus banksiana/P. resinosa*) group migrated northward from refugia on the coastal plain and in the Appalachians, as did fir (*Abies balsamea*). These four genera of conifers, arriving in New England from 12,000–11,000 yr. B.P. (Davis, 1983), were among the earliest trees to appear in the recently deglaciated region, and now have northerly distributions. However, jack pine is not presently a member of the Berkshire County flora.

White pine (*Pinus strobus*) and hemlock (*Tsuga canadensis*) persisted only along the coastal plain during glaciation. After glacial retreat, they migrated west to the Appalachians and then north into New England, arriving approximately 10,000–9000 yr. B.P. (Davis, 1983).

Deciduous trees, such as *Quercus, Ulmus, Acer, Carya* and *Castanea,* persisted in the south central portion of the United States and migrated north and eastward, but arrived in our area at widely varying times. *Quercus* reached New England about 10,000 yr. B.P., sugar maple (*Acer saccharum*) expanded into the northeast about 9000 yr. B.P., *Carya* migrated more slowly, and *Castanea* arrived only 2000 years ago, illustrating that present communities did not survive or migrate together (Davis, 1983). Our flora is made up of species which have been subjected to repeated dispersal, competition with many other species, and varying climatic conditions. Its composition undoubtedly is changing continuously, as the climate changes, as species continue to migrate, and as some perhaps become extinct in our area.

Berkshire County experienced total glaciation, the ice limit of the Wisconsin glacier being some 150 miles to the south and east. This glacial maximum occurred 20,000 yr. B.P. Climatic changes at the end of the last stadial (glacial period) resulted in rapid melting of the ice, the Berkshire County region becoming ice-free around 14,000 yr. B.P. (Davis and Jacobson, 1985; Whitehead, 1979).

Whitehead (1979) made a detailed study of the pollen profile in Berry Pond, a small natural pond in the town of Hancock,

Berkshire County, Massachusetts, at 610 m elevation in the Taconic Range. He found that the sedimentary record at this site began about 14,000 yr. B.P. and that it closely parallels pollen profiles seen in other New England bogs.

The lowest zone, or level of sediment, corresponding to about 13,000–12,100 yr. B.P., showed a large percentage of non-arboreal pollen, mostly Cyperaceae, and a very small pine component, either jack or red pine. Whitehead (1979) inferred an essentially treeless vegetation, somewhat comparable to tundra or forest-tundra.

The pollen profile of the next zone, from about 12,100–10,200 yr. B.P., indicated that spruce was dominant, pine not common, and alder (*Alnus*), juniper (*Juniperus* type), larch, fir, oak (*Quercus*) and hornbeam (*Ostrya/Carpinus*) were well represented. Presence of spruce has been corroborated by cones of white spruce (*Picea glauca*) found in a bog in Egremont, that were carbon-dated to 11,630 ± 470 yr. B.P. (Moeller, 1984). However, it is not possible to determine whether white spruce was the common spruce at that time; it is not native in Massachusetts at present.

The upper portion of this zone, in Whitehead's study, showed a decline of spruce and increase of pine and birch. Pine-pollen type indicated an increase of white pine (*Pinus strobus*). At about 10,500 yr. B.P., ash (*Fraxinus*), sugar maple, hazelnut (*Corylus*) and beech (*Fagus*) occurred in very small percentages. The presence of their pollen may not, however, indicate their actual presence in the flora. Miller and Thompson (1979) stated that temperate deciduous tree pollen appeared in very small quantities in many pollen profiles of this zone and may represent long-distance wind transport or rebedding. No macrofossils of *Quercus, Acer,* or *Ostrya/Carpinus* have been found in this zone in any New England site (Miller and Thompson, 1979).

Miller and Thompson's (1979) investigation of the Columbia Bridge site, near the Connecticut River in northern Vermont, yielded macrofossils dating from 11,540–11,390 yr. B.P., representing a rich assemblage of herbs and shrubs, but a low occurrence of spruce and balsam poplar (*Populus balsamifera*). This more northern site compared well with Whitehead's characterization of the same zone in Berkshire County as open boreal forest.

In the next zone in Whitehead's (1979) study, 10,200–8250 yr. B.P., pine and birch (*Betula*) were abundant. White pine predominated, but there was also some pitch pine (*Pinus rigida*) present.

Hemlock (*Tsuga canadensis*) made an appearance here as well and oak and the other deciduous trees increased in abundance.

Whitehead (1979) characterized the last zone, from 8250 yr. B.P. to the present, as the Oak-birch-beech-hemlock zone. Hemlock suffered a dramatic decline in his pollen profile, which corresponds to a similar decline noted all over the northeast around 4800 yr. B.P. (Davis et al., 1980). It was originally thought to be an effect of the Hypsithermal Period, but since only hemlock was affected, a disease or insect may have been the cause (Whitehead, 1979; Davis et al., 1980). Chestnut (*Castanea dentata*) arrived much later, about 2000 yr. B.P. in southern New England, and became an important part of the forest at Berry Pond along with white pine, pitch pine, hickory (*Carya*) and oak; this was a more southern type of assemblage than is seen today.

At present, red maple (*Acer rubrum*), red oak (*Quercus rubra*), and beech (*Fagus grandifolia*) are dominant in the forest around Berry Pond, reflecting historical disturbance, with sugar maple, yellow birch (*Betula alleghaniensis*), black cherry (*Prunus serotina*), paper birch (*Betula papyrifera*), and ash (*Fraxinus americana*) also common. Whitehead (1979) stated that the modern shrub and herbaceous layers of that site are not represented at all in his pollen profile. Other trees that do not produce abundant pollen or are less common today are also absent. A pollen profile reliably reflects only trees and shrubs that produce abundant pollen and are found within 15 km of the site of deposition (Davis, 1983). Whitehead (1979) also noted that since the Berkshires contain diverse topography and bedrock types, plant associations other than those described in his paper may have been present in the corresponding zones in different sections of the county.

## IV. FLORISTIC AFFINITIES

Repeated displacement of species during the Pleistocene, their migration back into regions of bare soil, and the subsequent mixing of species from quite different regions, from the boreal to the southern, and of different vegetational associations, has resulted in a present-day flora that may appear to be a confusing mixture. Davis (1983) termed the Eastern Deciduous Forest a "grab-bag of species" which was selected for colonization and competitive abilities. Perhaps this is one reason why the forest is able to renew itself after repeated clearing for timber and agriculture.

Each species exhibits an individual distribution, but patterns emerge that allow species with similar distributions to be assigned to a floristic group. Each group possesses a geographic "center" which gives it its name or affinity. The following floristic groups are recognized for Berkshire County: 1. the Eastern Deciduous Forest element (including a southern and midwestern element), 2. the Alleghanian element, 3. the Boreal element (including Circumpolar plants), 4. the Coastal Plain element and 5. an Alien element.

Examples of some common and characteristic species and of some rare plants are used to define each grouping. Affinities and migration patterns of the selected rare species are discussed more fully to illustrate the floristic relationships of Berkshire County flora. The use of the word "rare" is restricted to only those taxa listed by the Massachusetts Natural Heritage and Endangered Species Program (Sorrie, 1989) as rare in Massachusetts. Rare taxa that are found in the county are listed in Table 1, and are arranged according to affinity.

## Eastern Deciduous Forest Element

Since Berkshire County lies within Braun's (1950) Eastern Deciduous Forest, it is to be expected that plants of this phytogeographic element would be the most common and most important to the general character of the vegetation. These species have the wide distribution exemplified by *Corallorhiza odontorhiza* (Figure 1), although many extend farther north. They include most of our deciduous trees such as *Acer saccharum, A. rubrum, A. saccharinum, Quercus rubra, Q. alba, Prunus serotina, Tilia americana, Fagus grandifolia, Carya* spp., *Liriodendron tulipifera, Fraxinus americana, Ulmus* spp., and *Carpinus caroliniana.* On favorable soils a rich vernal flora is found typically with this forest. Fifteen common, spring wildflowers have approximately the same distribution, including *Hepatica nobilis* var. *obtusa* (*H. americana*), *Sanguinaria canadensis, Dicentra cucullaria, Erythronium americanum, Dentaria laciniata, Asarum canadense, Arisaema triphyllum, Thalictrum dioicum, Hydrophyllum virginianum, Geranium maculatum, Viola pubescens,* and *Thalictrum* (*Anemonella*) *thalictroides* (Gleason and Cronquist, 1964). The shrub *Dirca palustris* also has a similar distribution.

The plants of this widely distributed element that are consid-

Figure 1. Eastern Deciduous Forest element: distribution of *Corallorhiza odontorhiza* (after Luer, 1975).

ered rare (Sorrie, 1989), are so because they may require a more specialized habitat, or suffer from habitat elimination and commercial exploitation. Some, such as *Carex hitchcockiana* and *Blephilia hirsuta,* require a rich, mesic, calcareous soil. *Claytonia virginica,* rare congener of the common *C. caroliniana,* has narrower habitat requirements of rich, open floodplains. *Verbena simplex* and *Blephilia ciliata* occupy dry, calcareous open situations. The somewhat rich, open woods habitat of *Corallorhiza odontorhiza* (Figure 1) is fairly common, but the plant is scarce; what its particular needs are, are not fully known. Plants that inhabit an early successional vegetational type, such as a calcareous wet meadow, are easily shaded out by taller growth. *Ophioglossum vulgatum* and *Veronicastrum virginicum* are possible examples of rarity due to this process. *Panax quinquefolius,* while requiring rich sites, undoubtedly was more common before it became extensively hunted and the roots dug for herbal uses.

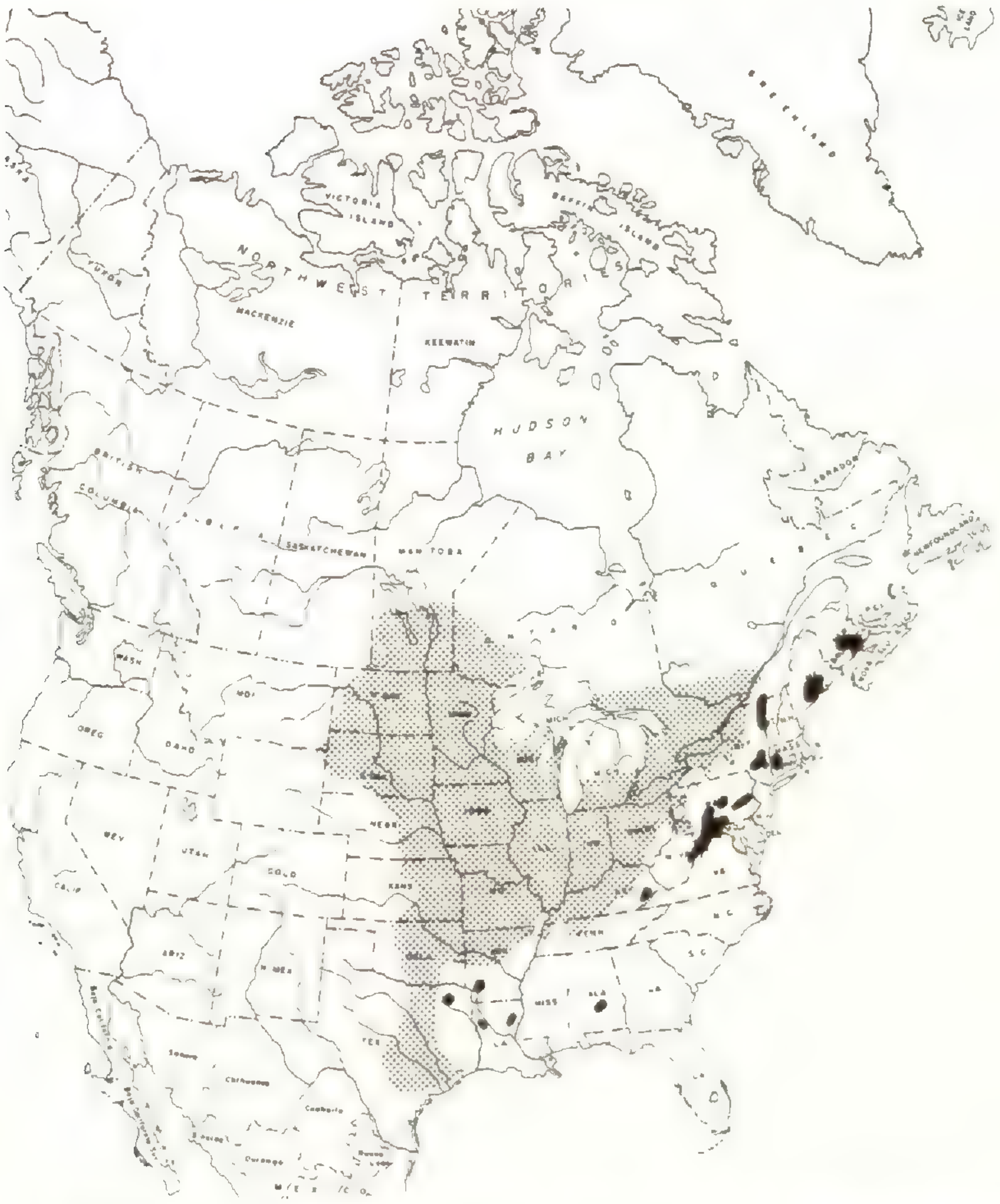


Figure 2. Southern-Midwestern element: distribution of *Quercus macrocarpa* (after Little, 1971).

A sub-group of the Eastern Deciduous Forest element has, from the point of view of the Berkshire County Flora, a distinctly southern and midwestern center (Figure 2). Most of these species are among the more uncommon or rare plants of the county as they are at or near the northeastern limits of their ranges, and most are found in the southern half of the county. Among these species are *Quercus macrocarpa, Q. muhlenbergii, Staphylea trifolia, Zanthoxylum americanum, Ilex montana, Solidago speciosa, Andropogon gerardii, Sorghastrum nutans* and *Chamaelirium luteum.*

Since the refugium of the deciduous forest species was centered in the south-central United States, migration spread northward and eastward. This sub-group probably migrated into Berkshire County along rivers, either from the Hudson River via the Hoosac River, and east along the Green and Williams Rivers, or north

along the Housatonic River, since there apparently existed little favorable habitat in the mountain ranges bounding the county.

Those plants that are at the eastern limits of their ranges may still be in the process of migrating eastward or northward as part of a continuing adjustment to the post-glacial period (Griggs, 1914). The rare *Ilex montana,* which occurs only in the southwest corner of the county, occupies a common type of acidic, rocky woodland. Its non-disjunct distribution may illustrate a continuing migration northeastward.

Certain species, such as *Quercus macrocarpa,* have outlying discontinuous distributions beyond their continuous area (Figure 2). Davis postulated (1965) that this species may have expanded its range during the Hypsithermal Period, 5000–4000 yr. B.P., then retreated as environmental conditions changed, leaving stranded populations.

Continued migration eastward may be impeded by several factors. Good (1974) indicated that a mountain range "athwart" the trend of migration is a more formidable barrier than one that is in the same alignment. The rare plant *Aster prenanthoides* reaches its easternmost limit in Berkshire County, where it is found primarily on the floodplains of two different rivers with separate watersheds: the Green River which flows east from New York State through the towns of Egremont and Great Barrington, and the Green River in Williamstown and Hancock, which rises near the New York–Massachusetts border. However, this species appears to be quite common on the western flanks of the Taconic Range, indicating that the two rivers provide migrational routes across the montane barrier. *Acer nigrum* may also migrate along rivers, since it is most often found in rich floodplain soil.

Other factors may affect migration. Increasingly unfavorable climate northward may impede further migration. *Asplenium montanum,* a rare fern, has no competition in its acidic, rocky-outcrop environment, which is not rare in the northeast, yet it is near its northeastern limit in Berkshire County. Habitat availability may limit *Chamaelirium luteum, Trichostema brachiatum* and *Lonicera hirsuta,* all rare species, since they need more sunlight than is found in the mature deciduous forest. *Chamaelirium luteum* inhabits more open, secondary woods, while the latter two species survive on open calcareous ledges. As Griggs (1940) suggested, many rare plants occupy natural pioneer habitats.

Edaphic conditions may form a barrier to migration. The many

calcicolous species at their eastern limit here in the county may be barred from migrating farther eastward by the acidic soils of the high, north-south trending Berkshire Plateau, as described by Egler (1940). Certain rare sedges found in calcareous fens, such as *Carex tetanica* and *C. schweinitzii,* or species of rich floodplains, such as *C. trichocarpa,* would find it difficult to spread eastward over this terrain which is not traversed by any suitable major river.

**Alleghanian Element**

Some species that are now an integral part of our flora belong to the Alleghanian element (Figures 3 and 4). They are confined to the area of the northeast and midwest which was once covered by the last glaciation, and extend southward along the Appalachian Mountains. Their refugia may have been on the coastal plain (Davis, 1983) and/or the Appalachian Mountains. Of this group, *Pinus strobus, Tsuga canadensis,* and *Betula alleghaniensis* are important members of the forest. *Betula alleghaniensis* is a co-dominant tree in the Northern Hardwoods Association (Küchler, 1964), particularly on the upper slopes. *Pinus strobus* is more prevalent at present in the southern half of the county, possibly due to greater abundance of well-drained soils and extensive agricultural disturbance associated with low, gentle topography. *Tsuga canadensis,* in the northern half of the county, occupies moist rocky ravines, north-facing slopes and poorly drained areas, while in the southern half of the county it is more widely distributed. Küchler (1964) indicated much of this southern section to be in a transition zone. *Pinus resinosa* occupies only a few mountain ridges in the southern half.

Trees of dry, sandy soil or rocky summits, *Pinus rigida* and *Quercus ilicifolia,* have similar, quite limited distributions in the Appalachian Mountains and in the northeast, especially near the coast. The pollen profile of Berry Pond indicated that *Pinus rigida* was more abundant around 4800 yr. B.P., during the Hypsithermal Period.

Because many Alleghanian species are largely restricted to areas formerly covered by the Wisconsin ice sheet, some authors (Braun, 1955) infer that the deciduous forest remained extant near the glacial edge, presenting a closed community that could not be

Figure 3. Alleghanian element: distribution of *Thuja occidentalis* (after Little, 1971).

invaded. An alternative explanation might be that many of these Alleghanian species could more easily colonize poor, poorly developed and bare soil than could typical Eastern Deciduous Forest species. In addition, the Eastern Deciduous Forest species, with their refugia in the south-central United States, were able to migrate rapidly northward into the unglaciated soil of the northern midwest (Davis, 1983). It may have then presented a closed community to the Alleghanian species spreading out from Appalachian refugia.

*Picea rubens,* now largely restricted to the Northeastern Spruce-Fir Forest (Küchler, 1964), is found on the highest mountain tops and ridges, and is associated there with *Abies balsamea,* a Boreal Forest species. The small tree or shrub *Rhus typhina* shows a typical Alleghanian distribution, as does the rare tree *Thuja occidentalis* (Figure 3). The rare plant *Clematis occidentalis* may

Figure 4. Alleghanian-Ozarkian element: distribution of *Rhynchospora capillacea* (after Gale, 1944).

occupy its habitat of open limestone ledges partly because, being a trailing woody vine, it cannot compete with typical deciduous forest growth.

Three rare plants, *Arabis lyrata, Cypripedium reginae* and *Rhynchospora capillacea,* illustrate an Ozarkian and Alleghanian distribution. These three species may have had refugia in both the Ozarks and the Appalachians during glaciation. The separate populations perhaps merged once they migrated northward, as in the case of *Arabis lyrata* and *Cypripedium reginae.* The Ozarkian population of *Rhynchospora capillacea* (Figure 4) may have migrated north to form the western stations while eastern stations may have derived from Appalachian refugia. *Arabis lyrata* is restricted to calcareous open ledges while *R. capillacea* and *C. reginae* are found only in calcareous fens, both uncommon habitats in Berkshire County.

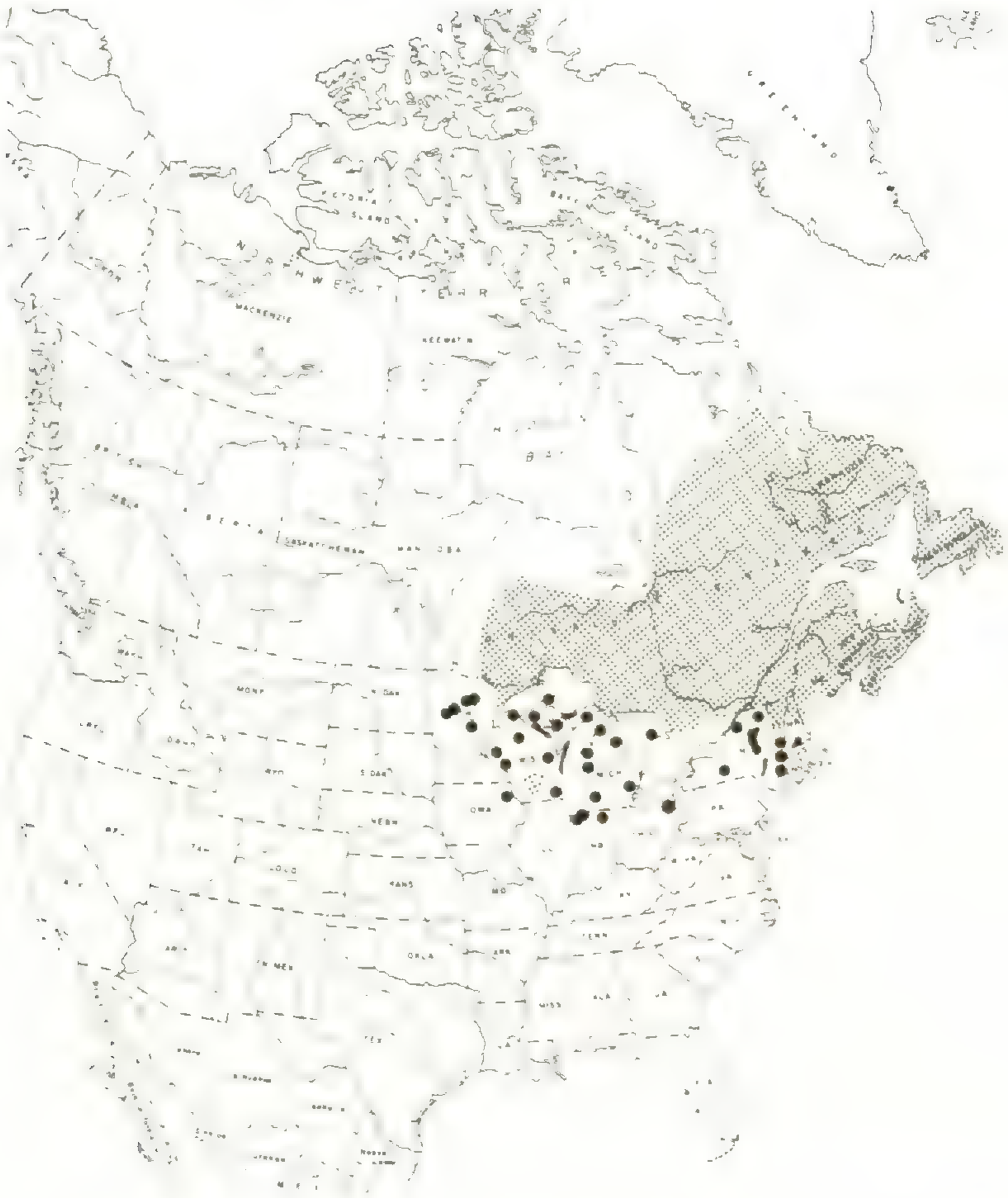

Figure 5. Boreal element: distribution of *Sorbus decora* (after Little, 1977).

**Boreal or Northern Element**

The Northern or Boreal element (Figure 5) contributes both important common species and rarer ones. Our common *Betula papyrifera,* although possessing a somewhat Alleghanian distribution southward, ranges far to the north where its distribution is transcontinental. *Betula cordifolia* is a member of the Northeastern Spruce-Fir Forest (Küchler, 1964) with *Abies balsamea,* the dominant tree species at the highest elevations (914–1064 m). *Larix laricina* and *Picea mariana* are found in cold bogs and fens. Many of our Boreal plants have a wide circumpolar distribution (Hultén, 1970), including *Epilobium angustifolium, Galium trifidum, Moehringia lateriflora, Circaea alpina, Chamaedaphne calyculata, Linnaea borealis, Menyanthes trifoliata* and *Viola selkirkii.*

As the Late Pleistocene climate warmed and the Wisconsin

Figure 6. Coastal Plain element: distribution of *Orontium aquaticum* (after Grear, 1966).

glacier retreated, Boreal species migrated upward in elevation and northward, resulting in some Boreal species being stranded as disjuncts, persisting today as rare plants in colder ravines, cold bogs and mountain tops in Berkshire County. *Vaccinium vitis-idaea* exists only as a single plant on a high exposed ledge. A few plants of *Polystichum braunii* occupy only in deep, cold ravines where there is a calcareous influence. *Woodsia glabella* inhabits a cool, high, shaded limestone ledge, of which there are few in the county. *Rosa acicularis* ssp. *sayi* is found on one open limestone ledge. The existence of these plants is tenuous since they occupy small habitat "islands" where they are subject to chance extinction. As Reznicek (1989) noted, many rare northern species occupy disjunct stations at their southern limit, as these species do. The probability of recolonization of such limited habitats is low because these sites are far from any replenishing source of

propagules. *Moehringia macrophylla* is absolutely restricted to serpentine outcrops, where it is locally abundant. *Amelanchier bartramiana, Sorbus decora* (Figure 5) and *Luzula parviflora* var. *melanocarpa* are components of the Boreal Forest on the summit of Mt. Greylock. *Solidago macrophylla* is found there as well as on several other mountain tops over 792 m.

Many of the plants considered to have northern affinities or to be circumboreal do not occupy strictly boreal habitats, but mix with more southern or widespread species. As discussed earlier, repeated displacement of vegetation by glacial advances has resulted in a flora derived from several affinities.

**Coastal Plain Element**

The few members of the Coastal Plain element (Figure 6) that occur in Berkshire County are generally found in the southern part of the county, although suitable soil and exposure also influence distribution. During the Wisconsin Glacial Period, the wide Continental Shelf was exposed between the ice sheet and the greatly lowered Atlantic Ocean. This area served as a refugium for many plants (Davis, 1965), some of which remained centered on the Coastal Plain after the glacier retreated and sealevel rose.

Taxa that exhibit Coastal Plain affinities are *Rhynchospora capitellata, Xyris difformis, Bartonia virginica, Utricularia radiata, Thelypteris simulata, Viola lanceolata, Juncus militaris,* and *Potamogeton confervoides.* The rare *Orontium aquaticum* (Figure 6), more typically found in Coastal Plain ponds, exists at one station in a sandy pond, as does *Juncus militaris.* These species chiefly occur in wet sands, acidic bogs or acidic waters of shallow ponds common on the Coastal Plain.

Coastal Plain species were undoubtedly able to migrate north readily from the Coastal Plain along the valleys of the south-flowing Housatonic, Farmington, and Westfield Rivers. Some species, particularly the aquatic taxa, may have been distributed by birds.

**Alien Element**

The Alien element of our flora is an important one, comprising approximately 25% of our species. Many were introduced purposely for pasture grass (*Phleum pratense, Dactylis glomerata*),

for herbal use (*Thymus serpyllum, Origanum vulgare*), for food (*Pastinaca sativa, Daucus carota*) and undoubtedly many for decorative use in gardens. Other species arrived by chance in grain, seed, wool, packing, ballast, clothing, railroads, automobiles, and food shipments; most were adapted to growing in disturbed soil and spread rapidly in the wake of tree clearance and agriculture. Many species, such as *Rhamnus cathartica* and *Alliaria petiolata,* have become more abundant since Hoffmann (1922) published his flora.

Additional species, not noted by Hoffmann, are still arriving and spreading rapidly; these include *Impatiens glandulifera, Rhinanthus minor, Euphrasia nemorosa, E. micrantha, Rhamnus frangula,* and a variety of grasses.

Removed from their own native competitors and predators, many species, such as *Lonicera morrowii, Alliaria officinalis, Lythrum salicaria, Rhamnus cathartica* and *R. frangula,* become pests and often choke out native vegetation. Others, such as *Leucanthemum vulgare* (*Chrysanthemum leucanthemum*), *Cichorium intybus, Centaurea maculosa, Ranunculus acris, Galium mollugo, Vicia cracca, Hieracium* spp., *Trifolium pratense* and the early-blooming *Tussilago farfara,* provide welcome color to meadows, roadsides and newly disturbed areas.

Several species, native to midwest or western North America, have expanded their range eastward into our region in response to extensive clearing by European settlers. *Rudbeckia hirta* var. *pulcherrima* is a common weed in pastures (Fernald, 1950), and *Penstemon digitalis* is occasional in moist meadows (Pennell, 1935; Fernald, 1950).

## V. SUMMARY

A variety of factors have influenced Berkshire County's floristic composition. Most important has been glaciation, which eliminated all pre-existing vegetation from the county and displaced the boreal and temperate vegetation southward. Many species may have been extirpated during repeated displacements. The survival of species in Pleistocene refugia and their post-glacial migration routes have largely determined the composition of our flora, which is a mixture of species with a variety of affinities. Species composition is undoubtedly still changing in response to this massive disturbance, and species may still be in the process

of either expanding their range or possibly becoming extinct in the county. Other factors affecting the composition and distribution of our flora are topography, bedrock geology, drainage and climate; these combine to provide diverse habitats for species with different affinities. These factors may also limit or promote plant migration. Certain taxa are at their southern, eastern or northern limits in the county.

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# RECURRENT APPEARANCE OF BISPORANGIATE STROBILI WITH PROLIFERATION ON *PICEA ABIES*

CHRISTOPHER A. TABOR

## ABSTRACT

Observations of mature Norway spruce, *Picea abies* (L.) Karst., that developed numerous bisporangiate strobili with proliferation were documented over a period of nine years. Most abnormal strobili had male characteristics at the proximal ends, female characteristics above, and vegetative proliferation at the distal ends. The degree of male, female, and vegetative characteristics varied among the hundreds of bisporangiate strobili observed, and there were many transitional stages. They appeared on one tree during eight spring-flushing seasons, on another during two seasons, and on five trees in the season following two environmental stresses: an insect infestation and a dry period which occurred when primordia were differentiating on developing embryonic shoots within buds.

Key Words: Norway spruce, *Picea abies,* bisporangiate strobili, vegetative proliferation, flowering, spruce mite, *Oligonychus ununguis,* environmental stress, Beltsville, Maryland

## INTRODUCTION

Shoot apical meristems of *Picea* and other genera of Pinaceae normally differentiate and develop to produce strobili with exclusively male, female, or vegetative characteristics. Occasionally, embryonic shoots develop as mixtures of two or three of these morphological types. The results may be bisporangiate strobili (true hermaphrodites containing characteristics of both sexes), or reproductive structures with vegetative proliferation. In the latter case, rudimentary needles may be interspersed with bracts and ovuliferous scales, or they may emerge from distal ends of strobili as terminal proliferation.

The earliest documentation of bisporangiate strobili in conifers was made by Dickson (1860). Since then, there have been many published reports of bisporangiate strobili, with and without proliferation, in different species. Few reports were of observations within the genus *Picea* (Chamberlain, 1935; Pauley, 1942; Santamour, 1959; Elliott, 1979), and all were of a single occasion. Some authors conducted detailed anatomical examinations (Tosh and Powell, 1986), and others reported on dissections of one or a few specimens (Bartlett, 1913; Kirkwood, 1916; Holmes, 1932; Looney and Duffield, 1958). This report documents the recurrent development of bisporangiate strobili with vegetative prolifera-

Table 1. Summary of the abundance of reproductive strobili on all Norway spruce trees on the site, and of bisporangiate strobili with proliferation on specific trees. (Specific trees are denoted by letters corresponding to the order of appearance of bisporangiate strobili. Abundance scale: 1 = very rare, 2 = rare, 3 = infrequent, 4 = abundant, 5 = very abundant.)

| Year of Observations | Abundance of Strobili on *Picea abies* | | | |
|---|---|---|---|---|
| | Reproductive Strobili on Trees on Site | | Bisporangiate Strobili on Specific Trees | |
| | Male | Female | Tree | |
| 1974 | 2 | 2 | A | 4 |
| 1975 | 4 | 2 | A | 3 |
| 1976 | 3 | 3 | A | 4 |
| 1977 | 2 | 1 | A | 2 |
| | | | B | 1 |
| 1978 | 5 | 3 | A | 4 |
| 1979 | 5 | 4 | A | 4 |
| | | | B–E | 3 |
| 1980 | 0 | 0 | A | 0 |
| 1981 | 4 | 2 | A | 2 |
| 1982 | 4 | 2 | A | 2 |

tion on mature trees of Norway spruce (*Picea abies* (L.) Karst.) observed during a period of nine years.

## METHODS

Annual observations were made on 27 mature, ornamental, Norway spruce trees that were planted in the 1930's at the Beltsville Agricultural Research Center, Beltsville, MD. The site had a gradually-sloping grade and well-drained soil. These and other trees in the locality had been observed and used as a source of embryonic shoots for anatomical and experimental studies since the early 1960's (Romberger, 1966; Varnell and Romberger, 1967; Romberger et al., 1970). The initial observations of bisporangiate strobili were made in May 1974, and continued each year thereafter, through June 1982. They were conducted at intervals throughout each spring-flushing period, under different daylight conditions, and with the aid of a telephoto lens. Some specimens were collected for photographing and closer examination, but most were left on the trees for continued observations. The abundance of reproductive strobili and bisporangiate strobili with proliferation were ranked on a numerical scale (Table 1).

Weather data collected for 27 years (1955 to 1982) at Beltsville Station No. 5 (located 1.6 km SSW of the site) were used to calculate the monthly means of the daily minimum, maximum, and average temperatures for each of the 9 years during which the trees were observed. In addition, long-term (27-year) monthly means of those parameters were calculated. Similarly, monthly precipitation values were summarized and long-term monthly means calculated. The 99% confidence interval for each monthly mean was determined by using the Student's *t*-distribution, and compared with individual monthly precipitation values from 1973 to 1982. Each month was classified as dry, normal, or wet, respectively, when the precipitation values were below, within, or above the confidence limits.

## OBSERVATIONS

The proximal ends of bisporangiate strobili were male, and had slender peduncles attached to pre-existing shoots. Distinct, bright yellow microsporophylls at different developmental stages were often present (Figures 1–3), and some microsporangia released pollen. Pollen grains from several strobili were tapped onto an agar nutrient medium, and their viability was confirmed by the germination and elongation of pollen tubes. Many strobili had rudimentary female structures with intensely purple ovuliferous scales in the mid-sections, and vegetative proliferation that consisted of distinct, small, green and yellow tufts of needles protruding from the distal ends (Figures 1 and 4). Some strobili were without a vegetative segment (Figures 2 and 5). Others had a variety of the anatomical gradients including mixed transitional features of both female and vegetative structures. Many variants of these patterns were observed, but even when female (Figure 5) or vegetative (Figure 6) structures were dominant, the attachments were by male-like peduncles. Consequently, few bisporangiate strobili remained attached to the trees for more than a few months. Only one predominately female bisporangiate strobilus was observed that developed coriaceous, brown, cone scales, but they were smaller than normal and were sterile.

In 1974, more than 100 bisporangiate strobili, many exhibiting proliferation, were observed on Tree A. This was a vegetative year for other trees on the site, and both male and female (microsporangiate and megasporangiate) strobili were ranked as rare

Figures 1–6. Examples of the diversity among bisporangiate strobili and vegetative proliferation observed. Prominent features are referenced in the text. **1.** From Tree A, 1974. .91×. **2.** From Tree D, 1979. .72×. **3.** From Tree A, 1976. .58×. **4.** From Tree C, 1979. .67×. **5.** From Tree B, 1979. .64×. **6.** From Tree A, 1974. 1.02×.

(Table 1). In 1977, bisporangiate strobili appeared on Trees A and B. During July 1978, all the trees were heavily damaged by the spruce mite (*Oligonychus ununguis*) and displayed classic symptoms of bleached and bronzed flecking and stippling on the

needles (Johnson and Lyon, 1976). September and October of that year were dry. During the subsequent growing season (1979), bisporangiate strobili with proliferation were observed on Trees A through E. In the summer of 1979, Kelthane (di(*p*-chlorophenyl)trichloromethylcarbinol) was applied to control another infestation of the spruce mite, and there was abundant precipitation during the summer and fall. During the following spring (1980), embryonic shoots were exclusively vegetative both on these trees and on trees located at nearby sites which were neither infested by the spruce mite nor sprayed with Kelthane.

## DISCUSSION

In Maryland, bud initiation in *Picea* begins in late April, during the period of elongation of the newly emerging shoot. By midsummer, newly initiated primordia accumulate and differentiate into distinctively vegetative, male, or female organs that constitute the embryonic shoots (Romberger, 1966; Owens and Molder, 1977; Harrison and Owens, 1983). During this period, the developing embryonic shoots are susceptible to influences that may direct and alter the course of differentiation in primordia. Environmental stress has been cited as a probable cause of bisporangiate strobili by Santamour (1959), who observed such structures on several species of *Picea* during the spring following a severe drought year. Elliott (1979) documented the appearance of bisporangiate strobili on *Picea mariana* in a forest-tundra ecotone, and hypothesized that development of these structures was caused by stress in the arboreally marginal environment.

Attempts were made to determine if the observations reported here were correlated with weather data, but no consistent trends were detected. In some years, however, there appeared to be a correlation between the amount of precipitation during the months of embryonic shoot development and the subsequent emergence of reproductive structures. This correlation was especially true for a period of abundant precipitation during the summer and fall of 1979, which was followed by the absence of reproductive strobili, including bisporangiate strobili, in the spring of 1980 (Table 1). In two other instances, reproductive strobili were abundant (1978 and 1979, Table 1) following dry months in the summer and fall. These dry periods coincided with the time of primordia differentiation on the developing embryonic shoots. In

addition, the spruce mite infestation during July 1978 imposed another environmental stress on the trees. This infestation, combined with the subsequent dry period, may have disrupted normal developmental sequences and resulted in the differentiation of various types of primordia on the embryonic shoots, as revealed when bisporangiate strobili with vegetative proliferation emerged from buds on five trees during the subsequent spring growth flush.

The recurrent development of bisporangiate strobili on one tree, and the fact that another tree of the same age and on the same site was predominately male during the years of observation, may reflect a genetic propensity for changes to occur in different degrees or at different rates among individuals. The differences may reflect phases of anatomical and sexual gradients that are characteristic within trees as they age (Prat, 1951). In that scheme, young trees have juvenile and sterile shoots, progress through male and female phases that include the appearance of hermaphroditic shoots, and culminate as old trees that may become purely male. Developmental changes expressed as anatomical gradients of sexual structures are probably associated with biochemical control mechanisms, such as altered concentration gradients of growth regulators, that may permit an established developmental sequence to change. These physiological gradients may be altered by stress in space over time.

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# THE GENUS *ANTENNARIA* (ASTERACEAE: INULEAE) IN ARCTIC NORTH AMERICA: CHROMOSOME NUMBERS AND TAXONOMIC NOTES

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## ABSTRACT

Chromosome numbers were determined from somatic material for 371 individuals representing 25 species of *Antennaria* from western and arctic North America. Most of the chromosome counts presented confirm previous reports for the respective taxa. Chromosome numbers are reported for specimens of *A. breitungii* ($2n = 56$), *A. ellyae* ($2n = 28$), *A. incarnata* ($2n = 56$) and *A. pedunculata* ($2n = 56$) collected from their respective type localities. Chromosome numbers are also reported for *A. pulcherrima* ($2n = 56$) and *A. rosea* ($2n = 70$) collected from their most northwestern stations in North America.

Key Words: *Antennaria*, chromosome numbers, northwestern North America

## INTRODUCTION

Much of the literature regarding chromosome number determinations for North American species of *Antennaria* has been summarized by Bayer and Stebbins (1987). Subsequently, chromosome number determinations were obtained from additional populations from both western (Chinnappa, 1986; Chmielewski and Chinnappa, 1988a) and arctic (Chmielewski and Chinnappa, 1988b) North America. At least a single chromosome count is now available for most of the North American species of *Antennaria*. Exceptions to this statement include many of the eastern arctic taxa of unsettled rank, as well as the endemic species *A. soliceps* Blake. Only a few species of *Antennaria* (i.e., *A. microphylla* Rydb., *A. rosea* Greene, and *A. umbrinella* Rydb.) have been examined in sufficient cytological detail to warrant substantiated cytogeographic discussion. Since only one study to date has concentrated on the determination of chromosome number for arctic taxa (Chmielewski and Chinnappa, 1988b), the aim of the present investigation is to supplement available chromosome number determinations for these arctic taxa so that cytogeographic discussions will be possible in the future.

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## MATERIALS AND METHODS

The methodology used here relative to cultivation and maintenance of specimens, as well as pretreatment of material for chromosome number determinations, has been described previously (Chinnappa and Chmielewski, 1987). Most of the major species groups in *Antennaria* from western arctic North America are problematic and warrant detailed systematic attention. Each of the major floras of the western arctic region (Anderson, 1959; Hultén, 1968; Welsh, 1974; Porsild and Cody, 1980) exhibits a particular bias in its respective taxonomic approach. Both Hultén (1968) and Welsh (1974) tended to lump species together into general groups while Anderson (1959) and Porsild and Cody (1980) tended to split these general groups into numerous species. In our study we did not accept either approach in its entirety, but used the available floras as a basis for specimen identification. Chromosome numbers are therefore reported separately for taxa which may ultimately be shown to be little more than minor variants in more diverse species complexes. The utilization of this approach was not intended to reflect support for recognition of these variants but is rather to serve as an informative aid to those investigators presently involved in revisions of these species complexes. A similar approach was adopted by Chmielewski and Chinnappa (1988b). The treatments of Chmielewski and Chinnappa (1988c) and Chmielewski et al. (1990a, 1990b) were followed for previously revised species complexes. All vouchers were collected by the authors and subsequently deposited at UAC.

## RESULTS AND DISCUSSION

Chromosome numbers were determined for 371 individuals representing 25 species (Table 1). Because species identification for arctic taxa is often based on the presence or absence of staminate plants in a population, chromosome numbers are reported separately for staminate and pistillate clones. Of the 25 species examined, 6 were represented by at least one population for which chromosome numbers were reported for both pistillate and staminate individuals. Most chromosome numbers reported for the respective species support previous determinations; thus they are presented without comment. Several groups of taxa remain problematic and as such warrant thorough systematic attention.

Table 1. Chromosome number determinations for 25 species of western North America *Antennaria* collected predominantly from north of the 60th parallel. Listed are species, chromosome number, location (KP = kilometre post, MP = milepost), and collection number. Staminate individuals are designated with an asterisk (*) following the collection number. A single hermaphroditic individual is designated with a double asterisk (**).

*A. alborosea* Porsild $2n = 56$. **Alaska**: Richardson Hwy.: 7 km N of Little Tonsina State Recreational Area, *3991*; MP 63, N of Chugach Mtns., N of Valdez, *3994*. Edgerton Hwy. to Chitina, 1.5 km E of Richardson Hwy. to Valdez, *4059*. **British Columbia**: Cassiar Hwy.: 10 km N of Cassiar, *4723*; Cassiar turnoff, 7 km W of Cassiar Hwy., *4724, 4725*; 12 km N of Iskut, just N of Tsasbye Creek, *4749A*. **Yukon**: Alaska Hwy.: 42 km W of Watson Lake, *3868*; 76 km W of Watson Lake, *3871*.

*A. angustata* Greene $2n = 56$. **Alberta**: Banff National Park: Parker Ridge Trail, *4885*; Sunshine Ski Resort Meadows, *4901, 4902, 4903*; Jasper National Park, just below summit of Mt. Edith Cavell Trail, *4892, 4893, 4894, 4895*. **British Columbia**: Haines Hwy., Three Guardsmen Pass, base of Three Guardsmen Mtn., KP 162.5, *3944*.

*A. atriceps* Fern. $2n = 56$. **British Columbia**: Haines Hwy.: Chilkat Pass, Nadahini Mtn., KP 147.7, *3957*; Stanley Creek, S of Yukon border, *3969, 3970*.

*A. breitungii* Porsild $2n = 56$. **British Columbia**: 7 km NE of Telegraph Creek, *4741*. **Yukon**: Klondike Loop 2, N of Carcross, S of Whitehorse, Lewes Lake, KP 136.3, (type locality) *3895, 3896, 3897, 3898, 3899*.

*A. compacta* Malte $2n = 56$. **Alberta**: Banff National Park, Peyto Lake Trail, *4879*. **British Columbia**: Haines Hwy.: S of Chilkat Pass, Mount McDonell, just S of Seltat Creek, KP 177.3, *3919*; Three Guardsmen Pass, base of Three Guardsmen Mtn., KP 162.5, *3947*.

*A. densifolia* Porsild $2n = 28$. **Yukon**: Dempster Hwy.: KP 131, N of Tombstone Mtn. Campground, *4519, 4520**; southern end of Windy Pass, KP 153.5, *4525, 4526**; northern end of Windy Pass, KP 177, S of Engineer Creek, *4535, 4536**; Windy Pass, KP 158.8, *4538**; Windy Pass, KP 157.9, *4540**, *4541*; S of Windy Pass, KP 130, *4544**, *4545, 4548**, *4549*.

*A. elegans* Porsild $2n = 28$. **Yukon**: South Canol Rd., just N of Bacon Creek, KP 179.5, *4669*.

$2n = 56$. **Alaska**: Richardson Hwy., 7 km N of Little Tonsina State Recreational Area, MP 68.5, *3993*. Edgerton Hwy.: to Chitina, 1.6 km E of Richardson Hwy. to Valdez, *4060*; 11.2 km N of Chitina, MP 25–26, *4067*. Old Edgerton Loop Rd., 13 km SE of intersection with Richardson Hwy., *4081*. Glenn Hwy., MP 181.1, Sheep Mtn. access rd., *4129*. Taylor Hwy., MP 16.5, NE of Tok, *4475*. **Alberta**: Hwy. 2, Huallen Rd., NW of Grande Prairie, *3761*. **British Columbia**: Alaska Hwy., N of Rancheria Falls, KP 1215.5, *3877*. Cassiar Hwy.: 6 km N of Boya Lake Provincial Park, *4721*; Telegraph Creek Rd., 5 km S of Dease Lake, *4730*; 12 km N of Iskut, *4749B*; 9 km N of Kinasken Lake Campground, *4757*. **Yukon**: Alaska Hwy.: 40 km W of Watson Lake, KP 1061.5, *3866*; 76 km W of Watson Lake, KP 1097.5, *3872*; Klondike Loop 2, Lewes Lake N of Carcross, KP 136.3, *3901*. Campbell Hwy., just N of turnoff to Frenchman Lake Campground, KP 552, *4607*; 10 km SE of Faro, KP 410, *4613*. South Canol Rd.: 2 km S of Lapie River crossing No.

Table 1. Continued.

2, KP 211.6, *4664*; KP 191.3, *4667*; Gold Creek, KP 177, *4670*; Teslin-Nisutlin Pass, KP 12.5, *4706*.

*A. ellyae* Porsild $2n = 28$. **Yukon**: Dempster Hwy.: Blackstone River, KP 131, *4521* (type locality); northern end of Windy Pass, KP 177, S of Engineer Creek Campground, *4537*.

*A. friesiana* (Trautv.) Ekman $2n = 28$. **Alaska**: Chena Hot Springs Rd., Chena Dome Trail, MP 49.1, NE of Fairbanks, *4237**, *4238*, *4240*; Manley Hot Springs Rd., MP 93.5, *4261**, *4262*. Dalton Hwy.: Department of Transportation Checkpoint, Chandalar Shelf, MP 237.1, *4295**, *4296A*, *4302*, *4303**; crossing No. 1, S of Atigun River, MP 253, *4340**, *4341*; 3.6 km N of Toolik Lake, MP 286, *4352**, *4353*; 3.6 km S of Pump Station No. 2, MP 357, *4405**; 8 km S of the Arctic Circle, MP 110–109, *4424**, *4425*, *4426**, *4427*; turnoff at Olsen's Lake and Kanuti Flats, just N of Finger Mtns., MP 98.2, *4428**, *4429*, *4430*. Steese Hwy.: Twleve Mile Summit, 0.8 km W of turnoff, MP 85.6, *4439**, *4440*; 1 km E of turnoff on Robert Pinnell Trail, *4444**, *4445*; Eagle Summit, 0.8 km E on Robert Pinnell Trail, *4451**, *4454*, *4455*, *4456**, *4457*, *4458**, *4459**. Taylor Hwy., turnout at top of summit, MP 143.3, *4491*.

$2n = 56$. **Alaska**: Dalton Hwy.: Department of Transportation Checkpoint, Chandalar Shelf, Brooks Range, MP 237.1, *4297*, *4301*; 3 km N of Island Lake, MP 278, *4347**, *4348*; 3.2 km N of Toolik Lake, MP 286, northern Brooks Range, *4351*, *4354*; 8 km S of Pump Station No. 2, MP 354, *4368*; 3.6 km S of Pump Station No. 2, MP 357, *4406*; 6.4 km N of Sagwon airstrip, MP 352, *4416*, *4417*. **Yukon**: Top of the World Hwy., just E of CAN–USA border, *4495*, *4498*, *4499*. Dempster Hwy.: 2 km N of Tombstone Campground, KP 74, *4506*; KP 107–108, beside Blackstone River, *4507*; southern end of Windy Pass, KP 130, *4550*.

$2n = 70$. **Alaska**: Richardson Hwy.: 7.7 km N of McCallum Creek, 35 km N of Paxson, *4083*; 3.7 km N of McCallum Creek, 31 km N of Paxson, *4089*; McCallum Creek, 27 km N of Paxson, *4090*; top of Chandalar Shelf, Department of Transportation Checkpoint, Brooks Range, MP 237.1, *4299*; 7.2 km N of Pump Station No. 3, MP 316, *4356*; 12.9 km N of Pump Station No. 3, Kakuktukruich Bluff, MP 320, *4358*; 11.2 km S of Pump Station No. 2, MP 352, *4363*, *4364*; 8 km S of Pump Station No. 2, MP 354, *4367*, *4370*; 6.4 km N of Sagwon airstrip, MP 352, *4418*.

*A. incarnata* Porsild $2n = 56$. **Yukon**: South Canol Rd., jctn. of Sheep Creek and Rose River, KP 153 (type locality), *4688*.

*A. isolepis* Greene $2n = 56$. **Alaska**: Richardson Hwy., 7 km N of Little Tonsina State Recreational Area, MP 68.5, *3992*. Glenn Hwy.: 6 km E of Little Nelchina River bridge, KP 227, *4109*; 5 km E of Eureka Summit, *4113*; just W of Eureka Summit, E of Tahneta Pass, *4125*; Sheep Mtn. access rd., KP 181.1, *4130*. Kenai Peninsula, jctn. of Shilak Lake Loop Rd. and Sterling Hwy., *4207*, *4208*. Shilak Lake Loop Rd., 12 km E of access rd. to Bottinentnin Lake, *4210*. George Parks Hwy.: Wilderness Rim Rd., N of Willow, MP 80, *4224*; southern part of ascent to Broad Pass, MP 97, *4227*. Taylor Hwy., MP 22.5, NE of Tok, *4477*. **British Columbia**: Haines Hwy.: Three Guardsmen Pass, base of Three Guardsmen Mtn., KP 162.5, *3946*; Chilkat Pass, Nadahini

Table 1. Continued.

Mtn., *3956*. Cassiar Hwy., 12 km N of Iskut, *4750*. **Northwest Territories**: North Canol Rd., 1.7 km N of Yukon border, *4653, 4655*. **Yukon**: Dempster Hwy., KP 40, *4503*. North Canol Rd.: just N of Mt. Sheldon, KP 363, *4625*; 1 km N of MacMillan River crossing, KP 414, *4639*; N of Dewhurst Creek, KP 430.5 *4643*; MacMillan Pass, MacKenzie Mtns., Backbone Range, KP 220, *4646*. South Canol Rd.: just S of Gold Creek, KP 177.2, *4675*; Lapie Lake access rd., *4678*; 1 km N of Groundhog Creek, *4681*; Rose River crossing No. 6, KP 155.1, *4684*.

*A. lanata* (Hook.) Greene $2n = 28$. **Alberta**: Banff National Park, summit of Parker Ridge, *4886*, 4887*.

*A. media* Greene $2n = 56$. **Alberta**: Banff National Park, summit of Parker Ridge Trail, *4884*. Jasper National Park, just below summit of Mt. Edith Cavell Trail, *4891*.

*A. microphylla* Rydb. $2n = 28$. **Alberta**: Ghost River Valley, *4907, 4908**. **British Columbia**: BC95, 2 km N of Edgermount, 12 km N of Radium, *4897*, 4898*.

*A. monocephala* DC. $2n = 28$. **Alaska**: Richardson Hwy.: Worthington Glacier, access rd. to recreational area, *4006*, 4007*; Thompson Pass, N of Valdez, just S of Blueberry Lake Recreational Area, *4039*, 4040, 4041*, 4042*; 4.8 km N of Thompson Pass, *4046*, 4047*; summit of Thompson Pass, *4050*, 4051, 4052*. Denali Hwy.: 1.5 km W of Paxson, *4094*; 5.6 km W of Paxson, *4095*, 4096*. Glenn Hwy., Eureka Summit, KP 208.1, *4116*, 4117, 4118**. Fishhook-Willow Rd., Hatcher Pass, NW of Palmer, *4140*, 4141*. Seward Hwy., Mount Alyeska, *4158*, 4159, 4160***. George Parks Hwy., southern end of ascent to Broad Pass, MP 97, *4226*. Steese Hwy.: 1.6 km E of turnoff on Robert Pinnell Trail, *4446, 4447, 4448*, 4449*; Eagle Summit, Robert Pinnell Trail, *4460*, 4461*, 4462*, 4463*, 4464, 4465*. **British Columbia**: Haines Hwy.: Three Guardsmen Pass, base of Three Guardsmen Mtn., KP 162.5, *3938*, 3939, 3940*, 3941, 3942*, 3943**; Stanley Creek, S of Yukon border, *3965*, 3966, 3967*, 3968*. **Yukon**: Nahanni Range Rd.: 32 km NE of Cantung Junction, Long Lake access rd., *3806*, 3807*; 90 km NE of Cantung Junction, between Moose Creek and Flood Creek, 10 km S of Flood Creek, *3822*, 3823*. Dempster Hwy., Tombstone Campground, nature trail W of campground, *4553*, 4554, 4555*. Silver Trail Hwy., Keno Hill Summit, Keno City, *4568*, 4569, 4570*. North Canol Rd., MacMillan Pass, S of roadpost 454, Mackenzie Mtns., Backbone Range, *4647*.

*A. neodioica* Greene $2n = 84$. **British Columbia**: Alaska Hwy., S of Tritch, KP 282, *3766*.

$2n = 112$. **Alberta**: Hwy. 43, 36 km NW of Whitecourt, *3754, 3755*. **British Columbia**: Pink Mtn. access road, 1 km W of Mae's kitchen, *3763*. Alaska Hwy., 15 km NW of Fireside, KP 897, *3787*. Cassiar Hwy., 9 km N of Kinasken Lake Campground, KP 379, *4754*. **Yukon**: Alaska Hwy., NE of Lower Post, KP 982, *3789*.

*A. oxyphylla* Greene $2n = 56$. **Alaska**: Elliott Hwy., MP 123.5, Manley Hot Springs Rd., *4279*; 16 km NE of Manley Hot Springs, *4282*. Dalton Hwy., N of Yukon River, hill marked 'Roller Coaster,' *4287*. Alaska Hwy., 6.5 km NW of Dot Lake, KP 1367.5, *4469*. Taylor Hwy., NE of Tok, KP 36.2, *4476*. **Yukon**: Klondike Loop, 5 km S of Pelly Crossing, KP 460, *4599*.

Table 1. Continued.

*A. pallida* Nelson $2n = 56$. **Alaska**: Richardson Hwy., Worthington Glacier, MP 28.7, *4008*. Valdez, 3.2 km along bay rd. from Alyeska Ferry terminal, *4027*. Edgerton Hwy. to Chitina, 1.6 km E of Richardson Hwy. to Valdez, *4061*. Denali Hwy.: 1.5 km W of Paxson, *4092*; 13.7 km W of Paxson, *4099*. Glenn Hwy., Eureka Summit, KP 208.1, *4119, 4120*. Mount Alyeska off of Seward Hwy., *4161*. George Parks Hwy., middle fork of Chulitna River, S of Broad Pass, MP 194.5, *4225*. **Alberta**: Jasper National Park, just below summit of Mt. Edith Cavell Trail, *4890*. **British Columbia**: Alaska Hwy., 2 km N of Strawberry Flats Campground, Muncho Lake, *3779*. **Yukon**: Nahanni Range Rd.: between North Moose Creek and Flood Creek, 10 km SW of Flood Creek, KP 89, *3819*; N of emergency airstrip, S of Ostensibility Creek, KP 119, *3830*.

*A. pedunculata* Porsild $2n = 56$. **Alaska**: Seward Hwy., Kenai Peninsula, just N of Hope access rd. turnoff, *4183*. Kalifornsky Beach Rd., just N of Kasilof, 19.3 km S of Soldotna, *4214*. Elliott Hwy., 6.4 km NE of Manley Hot Springs, MP 148, *4283*. Taylor Hwy., MP 15, NE of Tok, *4473, 4474*. **British Columbia**: Cassiar Hwy., 9 km N of Kinasken Lake Campground, KP 379, *4755*. **Northwest Territories**: North Canol Rd., 1.7 km N of Yukon border, *4654*. **Yukon**: Dempster Hwy.: Blackstone River area, KP 107.5 *4513*; Tombstone Campground nature trail, *4552*. North Canol Rd.: 0.5 km N of MacMillan River crossing No. 5, *4651, 4652*; N of Mt. Sheldon, KP 363, *4626*. South Canol Rd.: Rose River crossing No. 6, KP 155.1, (type locality), *4683, 4685*; jctn. of Sheep Creek and Rose River, KP 153, *4689*.

$2n = 70$. **Yukon**: North Canol Rd., N of MacKenzie River crossing No. 4, 0.7 km S of MacMillan River crossing No. 5, KP 459.6, *4650*.

*A. pulcherrima* (Hook.) Greene $2n = 56$. **Alaska**: Dalton Hwy.: 19.6 km N of Coldfoot, *4288*, 4289*; N of Coldfoot, Middle Fork Koyukuk River, bridge No. 1, *4293*, 4294*. **British Columbia**: Cassiar Hwy., 42 km N of Good Hope Lake, *4716**. **Yukon**: South Canol Rd.: jctn. of Sheep Creek and Rose River, KP 153, *4686*, 4687*; 1.5 km N of Rose River crossing No. 4, KP 145.8, *4692*, 4693*; just N of Rose River crossing No. 3, KP 144–143, *4695*, 4696*.

*A. rosea* Greene $2n = 56$. **Alaska**: Richardson Hwy.: just S of Tonsina River crossing, between Glenallen and Valdez, *3988*; N of Chugach Mtns., N of Valdez, just S of Tonsina State Recreational Area, *3995, 3996, 3997*. Glenn Hwy.: 1 km E of Tolsona Lake Rd., W of Tolsona Creek, *4101*; 10 km E of Tolsona Lake Rd., *4103*; 5 km E of Eureka Summit, *4112*; Sheep Mtn. access rd., KP 181.1, *4128*; E of Long Lake, KP 137.3, *4132*. Sterling Hwy., Kenai Peninsula, Shilak Lake Loop Rd., 1 km E of turnoff to Shilak Lake, *4206*. Elliott Hwy.: 4.8 km W of jctn. with Dalton Hwy., MP 77, *4257*; just SW of Baker Creek, MP 138, *4280*. Taylor Hwy., NE of Tok, MP 15, *4472*. **Alberta**: Hwy. 43, 2–3 km W of Valleyview, *3758*. Hwy. 2: W city limit sign for Grande Prairie, *3759, 3760*; Huallen Rd., NW of Grande Prairie, *3762*. **British Columbia**: Pink Mtn. access rd., 1 km W of Mae's Kitchen, *3764*. Alaska Hwy.: 21 km SE of Fireside, NW of Liard Hot Spring, *3782*; 10 km SE of Fireside, *3786*. Cassiar Hwy.: BC–Yukon border, KP 729.8, *4708*; 53 km N of Good Hope Lake, *4712*; 40 km N of Good Hope Lake, *4718*; 10 km N of jctn. to Cassiar, *4722*. Telegraph Creek Rd.: 5.5 km S of Dease Lake,

Table 1. Continued.

*4732*; 27 km S of Dease Lake, 1 km N of Auguste Childe Creek, *4734*; 17 km NE of Telegraph Creek, *4743, 4744*. Cassiar Hwy.: 24 km N of Iskut, *4748*; 12 km N of Iskut, *4751*; 9 km N of Kinasken, KP 379, *4756*. **Yukon**: NE of Lower Post, Hyland River crossing, *3790*. Nahanni Range Rd.: 4 km NE of Cantung Junction, *3792*; just N of North Bridge Creek, *3815, 3816*; between North Moose Creek and Flood Creek, KP 90, 10 km SW of Flood Creek, *3817*; N of emergency airstrip, S of Ostensibility Creek, KP 119, *3832*; between Ostensibility Creek and Piggott Creek, KP 125, *3843*. Alaska Hwy.: 40 km W of Watson Lake, KP 1061.5, *3865*; 42 km W of Watson Lake, KP 1063.5, *3867, 3869*; 76 km W of Watson Lake, *3870*; just N of Rancheria, *3874, 3875*. Klondike Loop 2, N of Carcross, Lewes Lake, *3894, 3900*. Haines Hwy., Kluane National Park, Auriel Trail, N of Kathleen Lake, *3913, 3914*. Top of the World Hwy., E of CAN–USA international border, KP 74–75, *4500*. Dempster Hwy.: KP 40, *4502, 4504*; Blackstone River, KP 109–110, *4515*; KP 12.2, *4562*. Silver Trail Hwy.: 1 km SW of jctn. to Minto Lake, KP 68, *4565, 4566*; Halfway Lakes, KP 77, *4567*. Just SW of jctn. of Duncan Creek Rd. and Silver Trail Hwy., SW of Keno City, *4595*. Duncan Creek Rd., 15 km NE of jctn. with Silver Trail Hwy., SW of Keno City, *4596*. Klondike Loop: between Mayo and Pelly Crossing, 20 km S of jctn. to Ethel Lake, KP 315, *4597*; 2 km N of MacGregor Creek, KP 406–407, *4603*. Campbell Hwy.: 21 km SE of Carmacks, KP 570, *4605*; 45 km NW of Faro, KP 465, *4612*. North Canol Rd.: Marjorie Lake area, *4615*; between Gravel Creek and Flat Creek, KP 281.3 *4618*; 2 km NE of Flood Creek, KP 308, *4619*; 3 km N of Dragon Lake, KP 338, *4621*; S of Itsi Range, KP 394, *4634, 4635, 4636*. South Canol Rd.: just S of Campbell Hwy., *4662*; S of Lapie River crossing No. 2, KP 191.3, *4666*; just S of Gold Creek, KP 177.2, *4671, 4672, 4673, 4674*; just N of Rose River crossing No. 3, KP 144–143, *4694*; N of Gravel Creek, KP 137.7, *4697, 4699*; 2 km N of Gravel Creek, KP 123.5, *4700*; just N of KP 112, *4701*; end of access rd. to Nisutlin River, KP 67.6, *4702, 4703*; Teslin-Nisutlin Pass, KP 12.5, *4705, 4707*.

$2n = 70$. **Alaska**: Richardson Hwy., 7 km N of Little Tonsina State Recreational Area, MP 68–69, *3990*. Elliott Hwy., 4.8 km W of jctn. with Dalton Hwy., MP 77, *4259*. Dalton Hwy., 16 km N of Yukon River Crossing, MP 66, *4286*. **Yukon**: North Canol Rd., N of Mt. Sheldon, KP 371, *4628*.

*A. sedoides* Greene $2n = 84$. **Alberta**: Banff National Park, summit of Parker Ridge Trail, *4880*.

*A. stolonifera* Porsild $2n = 56$. **Alaska**: 1 km SE of East Ave., SE of jctn. of Old Sterling Hwy. and Sterling Hwy., SE of Anchorage Pt., Kenai Peninsula, *4217*. **British Columbia**: Alaska Hwy., S of Tritch, KP 282, *3767*. **Yukon**: Nahanni Range Rd.: 32 km NE of jctn. with Campbell Hwy., Long Lake access rd., KP 32.7, *3804, 3805*; between North Moose Creek and Flood Creek, 10 km SW of Flood Creek, S of KP 89, *3818, 3820, 3821*; between Ostensibility Creek and Piggott Creek, KP 125, *3841*; 3 km NE of end of maintained section of road, KP 135, *3854*.

*A. straminea* Fern. $2n = 56$. **Alaska**: Glenn Hwy.: 6 km E of Little Nelchina River bridge, KP 227, *4110*; Eureka Summit, just W of summit, E of Tahneta Pass, *4124*. Kenai Peninsula, jctn. of Shilak Lake Loop Rd. and Sterling Hwy., *4205*.

Table 1. Continued.

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| *A. umbrinella* Rydb. $2n = 56$. **British Columbia**: Cassiar Hwy., S of Dease Lake, beside Day's Ranch, KP 88.5, *4737*. Telegraph Creek Rd., 7 km NE of Telegraph Creek, *4740*. |

**Monocephalous Taxa—The *Antennaria monocephala* DC. Complex**

This problematic group consists minimally of the monocephalous *Antennaria angustata* Greene, *A. monocephala* DC., *A. philonipha* Porsild, and *A. pygmaea* Fern. In North America, staminate specimens of these species (*A. monocephala* and *A. philonipha*) were consistently reported to be diploid (Chmielewski and Chinnappa, 1988b), whereas pistillate specimens were reported to be either diploid, triploid, pentaploid, or heptaploid (Packer and McPherson, 1974; Bayer and Stebbins, 1987; Chmielewski and Chinnappa, 1988a, 1988b). Polyploidy and the apparently associated shift from sexual reproduction to agamospermy are the two most likely factors that have contributed to morphological variation and related taxonomic confusion among these taxa; these evolutionary relationships are presently under investigation.

In previous taxonomic keys to these taxa, gender was considered to be a diagnostic character (Hultén, 1968; Porsild and Cody, 1980). However, gender ratios within a population, or an individual's gender *per se*, should have no bearing on its identification. Based on our preliminary results obtained from gender-independent morphometric analysis of quantitative characters, the monocephalous arctic *Antennaria* are treated as two taxa (Chmielewski and Chinnappa, unpubl.). Final decisions regarding the rank of these taxa await completion of examination of associated type material. The two taxa are treated herein at the specific rank (*A. angustata* and *A. monocephala*). Although similar in gross morphology, the two taxa differ in that the adaxial surface of both basal and cauline leaves in the former taxon is grey tomentose, whereas in the latter taxon, the surface is glabrous-strigose.

**Pleiocephalous Taxa—The *Antennaria friesiana* (Trautv.) Ekman Complex**

The problematic pleiocephalous taxa may be caespitose or stoloniferous. The caespitose taxa may be further subdivided into

those taxa in which the basal leaves are petiolated, lanceolate, spatulate, or spatulate-lanceolate, and those taxa in which the basal leaves are short, densely crowded, obovate to oblanceolate or obtuse. The first group of problematic pleiocephalous caespitose taxa consists of *Antennaria alaskana* Malte, *A. ekmaniana* Porsild, *A. friesiana* (Trautv.) Ekman, *A. neoalaskana* Porsild and *A. subcanescens* Ostf.—those taxa in which the basal leaves are petiolated, lanceolate, spatulate, or spatulate-lanceolate. Although a distinction was made between some of these taxa in previous studies dealing with chromosome number determinations (Johnson and Packer, 1968; Bayer and Stebbins, 1987; Chmielewski and Chinnappa, 1988b), we consider it prudent for the time being to include all specimens fitting these species descriptions under *A. friesiana s.l.* Based on a relatively small sample of arctic specimens, we previously believed that it was possible to separate these taxa on involucre size, achene characteristics and style length (Chmielewski and Chinnappa, 1988b). However, once a sufficiently large sample of specimens was examined, it became obvious that taxa once considered to be distinct represented end points of a morphological continuum. As with the monocephalous taxa, polyploidy (Table 1) and an associated shift from sexual reproduction to agamospermy are factors most likely responsible for taxonomic confusion in these taxa. Detailed evolutionary studies to determine associations among these taxa are presently underway.

In previously reported work (Chmielewski and Chinnappa, 1988b), we apparently misunderstood *A. crymophila* Porsild and erroneously reported diploid, tetraploid and pentaploid chromosome number determinations for seven individuals from arctic North America. These individuals are more appropriately treated as *A. friesiana s.l.*, and are so included here.

**Pleiocephalous taxa—The *Antennaria media* Greene Agamic Complex**

The second group of problematic pleiocephalous, caespitose taxa consists of *Antennaria compacta* Malte, *A. densifolia* Porsild and *A. ellyae* Porsild—those taxa in which the basal leaves are short, densely crowded, obovate to oblanceolate, or obtuse. Although the status of *A. compacta* is unsettled at present (Hultén, 1968; Welsh, 1968, 1974; Scoggan, 1979; Porsild and Cody, 1980),

there is little doubt that the taxon belongs in the *A. media* agamic complex. The three tetraploid counts listed for *A. compacta* (Table 1) support previous determinations for *A. media* (Bayer, 1984).

The diploid chromosome number listed in Table 1 for populations of *Antennaria densifolia* support previous determinations for this taxon from arctic North America (Chmielewski and Chinnappa, 1988b). Based on measurements of pollen grains and guard cells, Bayer (1989a) reported that a disjunct population of *A. densifolia* collected from Montana was also probably diploid.

Except for minor differences in plant height and stolon characteristics, specimens of *Antennaria ellyae* collected from the type locality were similar to *A. densifolia.* These diploid specimens were collected from beneath shrubs or in hollows which were either shadier or wetter than the surrounding exposed calcareous soils from which "typical" *A. densifolia* was collected. Morphological differences between the two taxa apparently reflect environmentally induced variation. Thus, although we consider *A. ellyae* to be synonymous with *A. densifolia,* the relationship between *A. compacta* and *A. densifolia* is under study.

*Antennaria atriceps* Fern., *A. pallida* Nelson, and *A. stolonifera* Porsild represent three stoloniferous, pleiocephalous taxa of unsettled rank (Porsild, 1950; Hultén, 1968; Welsh, 1968, 1974; Scoggan, 1979; Porsild and Cody, 1980), which, like *A. compacta,* belong to the *A. media* agamic complex. Additional studies are necessary to delimit evolutionary relationships among these taxa here included in the *A. media* agamic complex.

*Antennaria pedunculata* and *A. isolepis* remain as problematic taxa. Generally, *A. pedunculata* is most similar to *A. isolepis,* differing from the latter by its long-pedunculate lateral heads. The species is, however, similar to *A. isolepis* with respect to its broad, pale inner phyllaries. Although the involucres of *A. isolepis* are obviously pedunculate, the peduncles are generally less than two cm long and the lateral involucres do not overtop the central involucre. When lateral involucres overtop the central involucre, specimens of *A. isolepis* intergrade with *A. pedunculata.* Conversely, when peduncles are short and the inflorescence is compact, *A. isolepis* intergrades with *A. pallida.* A fourth taxon of unsettled rank associated with these species is *A. rousseaui* Porsild. We disagree with the placement of *A. isolepis* in synonymy with *A. rosea* subsp. *pulvinata* (Greene) R. Bayer (Bayer, 1989b) with the simultaneous exclusion of *A. pallida, A. pedunculata,*

and *A. rousseaui*. When a sufficiently large number of specimens is examined, a morphological continuum is apparent. As such, *A. isolepis, A. pallida, A. pedunculata* and *A. rousseaui* should not be dealt with independently. It is the opinion of the present authors that these species are more appropriately treated in the *A. media* agamic complex.

**Miscellaneous Complexes**

In addition to supporting and supplementing previous information on chromosome distribution in *A. pulcherrima* (Urbanska, 1983; Chinnappa, 1986; Bayer and Stebbins, 1987; Chmielewski and Chinnappa, 1988b), the present study lists tetraploid counts for pistillate and staminate individuals from the most northwestern known station for the species (Table 1).

*Antennaria rosea* was previously reported as diploid, triploid, tetraploid, and pentaploid (Bayer and Stebbins, 1981, 1987; Morton, 1981; Bayer, 1984; Chinnappa, 1984, 1986; Chmielewski and Chinnappa, 1988a, 1988b). The tetraploid and pentaploid chromosome number determinations presented for *Antennaria rosea* (Table 1) extend our previous knowledge of chromosome distribution for the taxon throughout the western arctic. Specimens examined from northern British Columbia fill a previous gap in our knowledge relative to the cytogeography of the species in this area. *Antennaria rosea* is predominantly tetraploid, but pentaploid individuals occur sporadically throughout its range (Chmielewski and Chinnappa, 1988c). A collection from the most northwestern station known for the species was pentaploid.

Three specimens could not be satisfactorily assigned to any of the western arctic species utilizing keys published by Porsild (1950), Anderson (1959), Hultén (1968), Welsh (1974), or Porsild and Cody (1980). Although they are similar to a paratype of *A. elegans* collected from the south end of Kluane Lake, Yukon (CAN *105589*), this specimen is not typical of that species. These three specimens more closely resemble the type of *A. straminea* Fern., a species considered to be endemic to Newfoundland, and are therefore reported under that name. The status of these collections, as well as of this species, warrant further investigation.

A sufficient number of chromosome counts is now available for most western arctic species of *Antennaria* to determine which cytotype is the more common in a species group. Chromosome

number determinations are lacking for eastern arctic species of *Antennaria*. Future cytological studies should deal predominantly with the eastern arctic and high arctic taxa. All the taxa of arctic North America warrant exhaustive morphological investigation. We are presently investigating both the *A. friesiana* and *A. monocephala* species complexes.

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# ADDITIONS TO THE FLORA OF THE ISLAND OF NEWFOUNDLAND

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## ABSTRACT

**Recent collections from Newfoundland have added the following vascular plant species to the native flora of the Island: *Brasenia schreberi, Carex tonsa, Dactylorhiza, Isoetes acadiensis, Lysimachia thyrsiflora, Myriophyllum farwellii, Potamogeton foliosus* var. *foliosus, Prenanthes racemosa, Sagittaria latifolia, Viola lanceolata,* and *V. ×sublanceolata.* Other novelties, including *Aster ciliolatus, Carex arcta, Eleocharis kamtschatica, Goodyera oblongifolia, Juncus subcaudatus,* and *Ranunculus lapponicus* are based on revisions of herbarium material. Significant changes to the known distribution of *Potamogeton spirillus* and *Utricularia purpurea* are also discussed. Additions based on published literature reports are also compiled for *Acorus americanus, Atriplex franktonii, A. praecox, A. subspicata, Carex cumulata, C. saxilittoralis, Euphrasia salisburgensis, Juncus ambiguus, Listera ×veltmanii, Potentilla bipinnatifida, Potamogeton strictifolius, Puccinellia ambigua* and *Sagina nodosa* ssp. *nodosa.*

Key Words: vascular plant flora, additions, Newfoundland

## INTRODUCTION

A comprehensive guide to the flora of Newfoundland has yet to be published. A first checklist of the vascular flora was compiled by E. Rouleau in 1949, followed by revised versions in 1956 and 1978. These lists comprise not only the flora of the island, but also comparative listings for Labrador and the adjacent French islands of St.-Pierre et Miquelon. They were based on that author's intensive research of records in major American and European herbaria, as well as his own extensive collecting on the Island from 1948 to 1972. Scott (1977) also published an updated checklist based largely on Rouleau's work.

Research on the flora of the west coast of the Island, particularly in Gros Morne National Park, has already contributed new additions to the flora, such as *Lycopodium alpinum* L. (Bouchard and Hay, 1974) and *Thelypteris limbosperma* (All.) H. P. Fuchs [syn.: *Oreopteris quelpaertensis* (C. Chr.) Holub] (Bouchard and Hay, 1976). Recent field studies, as well as examination of herbarium specimens and literature records made largely in the course of our research on the rare plants of the Island, have resulted in a number of new records which represent new additions to the flora of the province as compiled in Rouleau's list of Newfoundland plants (Rouleau, 1978).

In this paper we discuss eleven new records based on recent field collections. Six other novelties are the result of revisions of specimens in major herbaria with Newfoundland collections (CAN, CDFN, DAO, GH, MT, NFLD). Attention is drawn to two species that were previously known from only a single locality on the Island, but whose distribution has been substantially changed by our collecting. Fourteen additions or corrections are based on reports drawn from different sources, already published in the literature, but not included in Rouleau (1978).

Our comments are made with regard only to native species with the exception of *Dactylorhiza, Euphrasia salisburgensis* and *Sagina nodosa* ssp. *nodosa,* all of which appear to have been introduced from Europe.

Numerous species, most of which are based on doubtful literature records or misidentified herbarium specimens, may be excluded from the flora. These are being compiled in a forthcoming edition on the rare vascular plants of the Island of Newfoundland.

Botanists who are aware of other additions or deletions to the flora are encouraged to communicate their findings to us.

## ADDITIONS BASED ON RECENT COLLECTIONS

**Brasenia schreberi** Gmel.

This mainly eastern North American species ranges southward from the Gaspé and Nova Scotia to Florida, and inland to the Mississippi River basin. Sporadic occurrences further to the west, and elsewhere throughout the world, as well as fossil evidence, seem to indicate a much reduced present-day range from a former cosmopolitan Tertiary distribution (Raymond and Dansereau, 1953). The recent discovery of this distinctive aquatic plant in an oligotrophic pond north of Bonne Bay in Gros Morne National Park constitutes the northernmost locality in eastern North America (map, Fleurbec, 1987).

SPECIMENS. St. Barbe South Distr.: Berry Hill, Buck Pond, 1989/07/25, *Bouchard & Hay 89291* (CAN, MT).

**Carex tonsa** (Fern.) Bickn.

*Carex tonsa* [syn.: *C. umbellata* Schk. *ex* Willd. var. *tonsa* Fern., *C. rugosperma* Mack. var. *tonsa* (Fern.) E. Voss] has not been

reported from Newfoundland, although the closely related *C. abdita* Bickn. (syn.: *C. umbellata sensu* Mack., *non* Schk. *ex* Willd.) is known from the Island (Robertson, 1984; Rouleau, 1978). There is some disagreement about the circumscription of these taxa (Gleason, 1963), but *C. tonsa sensu str.*, with its stiff, thick, rigid leaves and glabrous (or nearly so) perigynia, appears quite distinctive. It has been recently collected from two localities in north-central Newfoundland, where its habitat of dry, open siliceous soils is encountered.

SPECIMENS. Bonavista North Distr.: Pine Acres, Grants Siding, 1988/07/20, *Bouchard, Hay & Brouillet 88091* (CAN, MT). Green Bay Distr.: Davis Brook, Springdale, 1988/07/25, *Bouchard, Hay & Brouillet 88219* (CAN, MT).

## Dactylorhiza

*Dactylorhiza* is an extremely variable orchid genus of at least thirty species and many hybrids and intermediate forms, found primarily in the Old World (Case, 1987; Luer, 1975). Only two species have been reported to occur in North America, *D. aristata* (Fischer) Soó, in the Aleutians and the Alaskan Peninsula, and *D. maculata* (L.) Soó, widespread in Europe and believed to be adventive at a single locality near Timmins in northern Ontario (Case, 1987; Luer, 1975; Whiting and Catling, 1986). A small population of 10 plants of this genus was found recently at Tilt Cove in a springy area along a small brook near ruined house foundations in the abandoned mining town. They were probably introduced as garden plants from Europe when the copper mine was active (1864–1946, British financial interests), and have persisted locally. With photographs taken in the field, and comparison of the collections with European herbarium specimens, the plants have been tentatively identified as belonging to the *D. incarnata* (L.) Soó species complex. Unlike the Ontario plants, which have been placed in the *D. maculata* complex, the Tilt Cove specimens have hollow stems, unspotted lanceolate basal leaves, and distinctly suberect lateral sepals. This would be the first report of the *D. incarnata* group in North America. There is much confusion in recognition of species in the dactylorchids; their complex taxonomy has been discussed recently by Bateman and Denholm (1985, 1988).

SPECIMENS. Green Bay Distr.: Tilt Cove, 1988/07/26, *Bouchard, Hay & Brouillet 88282* (CAN, MT).

**Isoetes acadiensis** Kott

This quillwort was described as a new species from eastern Canada by Kott (1981). It is known from New England, New Brunswick and Nova Scotia. Recent collections and revision of herbarium material from the Salmonier area by D. Britton have added this relatively unknown aquatic species to the flora of Newfoundland.

SPECIMENS. St. Mary's Distr.: Salmonier, 1965/08/13, *Rouleau & Smith 9843* (MT), Salmonier River: 1981/08/10, *Britton & Medhurst 8596B* (OAC); 1982/07/28, *Britton & Anderson 9011a* (OAC). Deer Park, Oxley's Pond, 1982/07/28, *Britton & Anderson 9019b* (OAC).

**Lysimachia thyrsiflora** L.

This wide-ranging, circum-temperate species was discovered recently along the banks of the Upper Humber River, near Deer Lake. The northeastern limit of this taxon in the Gulf of St. Lawrence is on adjacent Anticosti Island, at a similar latitude. It has been reported further north from Goose Bay, Labrador, but Rousseau (1974) refuted this claim. Other rare species found along the Upper Humber River at the same locality include *Alisma plantago-aquatica* L., *Callitriche hermaphroditica* L., *Myriophyllum verticillatum* L., *Potamogeton foliosus* Raf., *P. spirillus* Tuckerm., *Sagittaria latifolia* Willd., and *Utricularia purpurea* Walt.

SPECIMENS. Humber East Distr.: Deer Lake Park, 1972/07/17, *Green 1883* (CDFN). Upper Humber River, Deer Lake, 1988/07/28, *Bouchard, Hay & Brouillet 88328* (CAN, MT). Riedville, Upper Humber River, 1989/07/10, *Bouchard, Hay & Brouillet 89002* (CAN, MT).

**Myriophyllum farwellii** Morong

The distribution of this species of water milfoil is centered mainly around the Great Lakes region, but eastward it ranges from northern New England to Nova Scotia. Crow and Hellquist (1983) first mentioned its presence in Newfoundland on the basis of their discovery of it at a single locality on the Avalon Peninsula. It was found growing at the margin of an acidic pond in a sphagnum bog.

SPECIMENS. Harbour Main Distr.: Avalon Peninsula, east of Whitbourne: 1979/

07/08, *Crow & Hellquist 13361* (NASC); 1988/07/15, *Bouchard, Hay & Brouillet 88034* (CAN, MT).

**Potamogeton foliosus** Raf. var. **foliosus**

This taxon has a transcontinental temperate range, although it occurs sporadically as far north as Alaska and Great Slave Lake (map, Haynes, 1974). It has been found at only one locality in Newfoundland, which represents the northeastern limit of the range. The plants were growing in shallow, dead waters along the Upper Humber River, along with other rare aquatics including *Callitriche hermaphroditica, Myriophyllum verticillatum, Potamogeton spirillus* and *Utricularia purpurea.* The specimens were mixed with collections of *P. pusillus* L. var. *tenuissimus* Mert. & Koch, as determined by B. Hellquist.

SPECIMENS. Humber East Distr.: Upper Humber River, Deer Lake, 1988/07/28, *Bouchard, Hay & Brouillet 88317a* (MT, NASC).

**Prenanthes racemosa** Michx.

Fernald (1925) included *P. racemosa* among the Cordilleran elements disjunct to the Gulf of St. Lawrence. It is now known to have a transcontinental boreal distribution (Scoggan, 1978–79). In Newfoundland it was recently discovered near Corner Brook, in a fen with other rare species such as *Cypripedium reginae* Walt. and *Valeriana septentrionalis* Rydb. The closest localities, at the northeastern limit of the range of the species, are found on the Québec North Shore (Lavoie, 1984).

SPECIMENS. Humber East Distr.: Wild Cove, 1987/08/07, *Brouillet & Saucier 87582* (CAN, MT).

**Sagittaria latifolia** Willd.

In eastern North America, this species ranges along the Atlantic coastal plain, occurring sporadically in the southeast and then continuously from Virginia north to Nova Scotia. It is frequent inland as far as the Midwest, from where the range is disrupted to the Pacific coast (map, Bogin, 1955; Fleurbec, 1987). It was first reported in Newfoundland from a marsh near Stephenville (Mann, 1986). Additional stations have recently been found along

the marshy banks of the Upper Humber River near Deer Lake. These are the northernmost localities on the eastern seabord.

SPECIMENS. Humber East Distr.: Upper Humber River, Deer Lake: 1988/07/28, *Bouchard, Hay & Brouillet 88308, 88327* (CAN, MT); 1989/07/10, *Bouchard, Hay & Brouillet 89001* (CAN, MT). Port au Port Distr.: Stephenville Crossing, Little River, 1986/08/06; *Mann s.n.* (NFLD).

**Viola lanceolata** L.

This species occurs mainly in the Great Lakes–St. Lawrence region, the eastern coastal states and the Maritimes (map, ssp. *lanceolata,* Russell, 1965). Although known from the adjacent French islands of St.-Pierre et Miquelon (LeGallo, 1954), it has not been reported previously from Newfoundland. It has been collected at two localities at the head of Placentia Bay where it was found growing on the open moist sandy floodplains of two rivers, hybridizing freely with *V. pallens* (Banks) Brainerd (see discussion under *V.* ×*sublanceolata*).

SPECIMENS. Placentia West Distr.: Sandy Harbour River: 1972/08/25, *Rouleau & Rast 11315* (MT); 1988/07/16, *Bouchard, Hay & Brouillet 88046* (CAN, MT). Trinity North Dist.: Piper's Hole River, 1983/07/04, *Favreau s.n.* (NFLD).

**Viola** ×**sublanceolata** House

*Viola pallens* (syn.: *V. macloskeyi* Lloyd var. *pallens* (Banks) Hitchc.) and *V. lanceolata* ssp. *lanceolata* are known to produce a usually sterile $F_1$ hybrid. Russell (1965) reported such hybrid plants from Minnesota, Wisconsin, Michigan, and New England, and it is known from southern Ontario and Québec (Scoggan, 1978–79). In Newfoundland, it was recently found growing in a mixed population with the parent species.

SPECIMENS. Placentia West Distr.: Sandy Harbour River, 1988/07/16, *Bouchard, Hay & Brouillet 88051* (CAN, MT).

## ADDITIONS BASED ON REVISIONS OF (MISIDENTIFIED) HERBARIUM SPECIMENS

**Aster ciliolatus** Lindl. *ex* Hook.

The only specimens of this species from Newfoundland constitute the type collection of *A. foliaceus* Lindl. var. *subgeminatus*

Fern. (Fernald, 1915). The latter taxon is not mentioned in Fernald (1950), Scoggan (1978–79, who also specifically states "*A. ciliolatus* . . . not known from Nfld . . ."), nor Gleason and Cronquist (1963). Boivin (1948) elevated it to species rank (*A. subgeminatus* (Fern.) Boivin), while Jones (1980) expressed the opinion that the latter is a nothotaxon and represents the hybrid *A. tardifolorus* ×*ciliolatus* (*Aster tardiflorus* was later placed by Jones in *A. novi-belgii* ssp. *tardiflorus*). Boivin (1966–67) and Rouleau (1956, 1978) mentioned *A. subgeminatus* as occurring in Newfoundland, but not *A. ciliolatus*. However, Fernald (1949) recognized the relationship of var. *subgeminatus* to *A. ciliolatus*: "var. *subgeminatus* . . . being the endemic western Newfoundland representative of *A. ciliolatus* . . . ," a statement missed by all floristicians subsequently dealing with the Newfoundland flora who apparently associated the variety to *A. novi-belgii* (and its synonyms *A. foliaceus* auct., *A. subspicatus* auct., *A. johannensis*, etc.). In the course of a biosystematic study of *A. novi-belgii* in the northeast (Labrecque, 1990, mém. M.Sc., Univ. de Montréal), the type of var. *subgeminatus* was examined and determined to be within the range of variation of *A. ciliolatus* (Brouillet, 1981, Ph.D. thesis, Univ. of Waterloo), and not a hybrid with *A. novi-belgii*, even though the latter is abundant in the area. In Newfoundland *A. ciliolatus* is very rare, being known from a single locality and not collected since 1910.

SPECIMENS. Port-au-Port Distr.: Table Mountain, 1910/08/16, *Fernald, Wiegand & Kittredge 4126* (GH).

**Carex arcta** Boott

This mainly boreal North American sedge is known from only one locality in the Long Range Mountains. Originally misidentified and distributed as *C. brunnescens* (Pers.) Poir., the proper identity of this herbarium sheet has been recognized only recently.

SPECIMENS. St. Barbe South Distr.: Highlands of St. John's, Doctor Hill, 1929/07/31, *Fernald, Long & Fogg 1395* (GH, MT).

**Eleocharis kamtschatica** (C. A. Meyer) Komarov

Specimens belonging to the *Eleocharis uniglumis* complex have been collected from two localities on the limestone barrens along the northwest coast of the Island. The material was originally

misidentified as *E. pauciflora* (Lightf.) Link and *E. halophila* (Fern. & Brack.) Fern. & Brack. Both collections are immature; however, they can be assigned with certainty to the *E. uniglumis* complex (P. Ball, pers. comm.). Although Fernald (1950) had reported *E. uniglumis* (Link) Schultes for Newfoundland, Svenson (1947) discounted the specimen (Blomidon Mountains; *Fernald & Wiegand 2706,* GH) stating that the collections "are not uniglumate at all, and . . . perfectly typical *E. smallii* Britt." Nearly identical collections from a similar habitat in eastern Québec (Rivière Romaine; *Marie-Victorin & Rolland-Germain 20165,* MT) have been referred to *E. kamtschatica* (Dutilly et al., 1958; Svenson, 1947), an amphi-Beringian species with disjunct localities eastward in northern Ontario (James Bay), Québec and Labrador (Ball and White, 1982). We are tentatively referring the Newfoundland collections to this taxon.

SPECIMENS. St. Barbe South Distr.: Pointe Riche, 1929/07/24, *Fernald, Long & Fogg 1338* (GH, MT). Portland Creek, Eastern Head, 1974/07/14, *Hay & Bouchard 7472* (CAN, MT).

**Goodyera oblongifolia** Raf.

This species is primarily a western taxon with disjunct eastward centers of distribution around the Great Lakes and in southern Québec. Isolated populations occur in New Brunswick, Nova Scotia and Vermont (map, Kallunki, 1976). It is very rare in Newfoundland where it is now known from a single locality at Serpentine Lake. The specimen was misidentified as *G. tessellata* Lodd. This addition represents an important extension to the northeastern extreme of the species range.

SPECIMENS. Humber West Distr.: Serpentine Lake, 1955/08/10, *Rouleau 4086* (MT, NFLD).

**Juncus subcaudatus** (Engelm.) Coville & Blake

In North America *J. subcaudatus* is found mainly in the central part of the Atlantic coastal plain from where its range extends southward through the Appalchian uplands to northern Georgia, and northward to disjunct southern Nova Scotia (Hay, 1984). The Nova Scotian plants have been segregated as an endemic variety, var. *planisepalus,* by Fernald (1921). A revision of herbarium material from the Maritimes has revealed new outlying

locations in Newfoundland and St.-Pierre et Miquelon, which represent an important extension to the northeast of the species' known distribution. These localities are widely scattered on the Island, a pattern shared by several of the coastal plain elements such as *Bartonia paniculata* (Michx.) Muhl., *Hudsonia ericoides* L., *Juncus militaris* Bigel. and *Schizaea pusilla* Pursh.

SPECIMENS. Grand Falls Distr.: Grand Falls: 1911/08/11, *Fernald, Wiegand & Darlington 5127* (GH, MT); Exploit's River, 1911/08/12, *Fernald, Wiegand & Darlington 5128* (GH). Green Bay Distr.: Sheffield Lake, Southwest Brook, 1951/08/16, *Rouleau 2512* (DAO, MT). St. Mary's Distr.: Peters River, 1949/09/17, *Rouleau 5156* (MT).

**Ranunculus lapponicus** L.

*Ranunculus lapponicus* has a general subarctic-boreal circumpolar range. In eastern North America it is found sporadically throughout northern and central Québec/Labrador with isolated, rare occurrences southward in New Brunswick and Maine. A revision of herbarium specimens has revealed a new locality in Newfoundland in the highlands southeast of Deer lake.

SPECIMENS. Humber East Distr.: Grand Lake, mountain top, 1956/07/25, *Wilton 302* (CDFN).

## NOTEWORTHY CHANGES TO KNOWN DISTRIBUTIONS

**Potamogeton spirillus** Tuckerm.

Ranging from Nova Scotia through New England and the Middle Atlantic States to the Great Lakes (map, Reznicek and Bobbette, 1976), this easily overlooked pondweed has been previously recorded only from Grand Falls, where it was collected by Fernald in 1911. We have recently expanded its distribution on the Island with several widespread collections.

SPECIMENS. Humber East Distr.: Upper Humber River: Deer Lake, 1988/07/28, *Bouchard, Hay & Brouillet 88320* (MT); Riedville, 1989/07/10, *Bouchard, Hay & Brouillet 89005* (CAN, MT). Grand Falls Distr.: Grand Falls, Rushy Pond: 1911/08/11, *Fernald, Wiegand & Darlington 4492* (CAN, GH); 1988/07/22, *Bouchard, Hay & Brouillet 88147)* (CAN, MT). Gander Distr.: Exploit's River, Bishop's Falls, 1988/07/23, *Bouchard, Hay & Brouillet 88189* (CAN, MT). Fortune Bay Distr.: Northwest Gander River, 1988/07/23, *Bouchard, Hay & Brouillet 88174* (MT), *88177* (CAN, MT, NASC).

**Utricularia purpurea** Walt.

*Utricularia purpurea* ranges from Newfoundland and Nova Scotia, west to southern Ontario, northern Indiana, Michigan and Wisconsin, and south along the Coastal Plain to Florida, Louisiana and Texas (Crow and Hellquist, 1985). This rare bladderwort has been recorded only from around Colinet (St. Mary's Distr.) on the Avalon Peninsula (Smith, 1966). Our collections from several widespread stations rectify this misconception.

SPECIMENS. Humber East Distr.: Upper Humber River, Deer Lake, 1988/07/28, *Bouchard, Hay & Brouillet 88309* (MT). St. Mary's Distr.: Island Pond, Colinet, 1965/08/13, *Smith 320* (MT, NFLD); 1965/09/20, *Smith 368* (NFLD), *369* (NFLD), 1969/04/13, *Smith 455* (NFLD); 1988/07/14, *Bouchard, Hay & Brouillet 88027* (CAN, MT). Salmonier Line, no date, *Wells 1774* (CDFN). Fortune Bay Distr.: Harbour Breton Road, Conne River, 1989/07/18, *Bouchard, Hay & Brouillet 89275* (CAN, MT).

## ADDITIONS BASED ON REPORTS IN PUBLISHED LITERATURE

**Acorus americanus** (Raf.) Raf.

This taxon, which was recognized in Newfoundland by Packer and Ringius (1984) and which is known from only one locality on the Grand Codroy River, had been reported previously as *A. calamus* L. (Rouleau, 1978). The latter taxon is the sterile European triploid which has been introduced sporadically in North America, but apparently not in Newfoundland. *Acorus americanus* is the correct name for the fertile diploid species in North America (Packer and Ringius, 1984).

**Atriplex franktonii** Taschereau

This species was reported by Basset et al. (1983) in the region of Bay Roberts, Conception Bay. However, P. Taschereau (pers. comm.) expressed doubt about the validity of this report and we have been unable to substantiate it. *Atriplex franktonii* is restricted to coastal beaches of New Brunswick, Prince Edward Island and Nova Scotia (Taschereau, 1972).

**Atriplex praecox** Hülphers

This species is a poorly understood amphi-Atlantic taxon which has only recently been reported from several widely scattered

coastal localities in Newfoundland by Thannheiser (1981, 1984), and which has only been recently recognized in the flora of the Maritime Provinces (Bassett et al., 1983). The specimens were identified by P. Taschereau.

**Atriplex subspicata** (Nutt.) Rydb.

This species was only recently recognized in eastern North America (Taschereau, 1972). It occurs along the Atlantic coast from the St. Lawrence River south to Massachusetts and inland in western Canada and United States. Some collections in Newfoundland that heretofore have been assigned to *A. patula* L. or *A. patula* var. *hastata* A. Gray, have been treated as *A. subspicata* by Bassett and Crompton (1973), Bassett et al. (1983) and Thannheiser (1981, 1984). It occurs at several widely scattered coastal localities.

**Carex cumulata** (Bailey) Mack.

This east-temperate member of the section *Ovales* ranges from southern Manitoba to Nova Scotia and southward from Michigan to New Jersey. Not previously known from Newfoundland, it has been recorded by Robertson (1984) from a single locality (Gambo, Bonavista North Distr.), where it may have been introduced. Confusion in delineating segregates in the complex surrounding *C. cumulata* led Boivin (1979) to regroup this species with *C. brevior* (Dewey) Mack. We have not been able to verify the voucher specimen.

**Carex saxilittoralis** A. Robertson

Endemic to Atlantic Canada, this diminutive sedge of the *Carex viridula* group was first discovered and described by Robertson (1980) on the basis of specimens from coastal limestone gravels at Bellburns, St. Barbe South Distr. It is known at several coastal localities around the Island (map, Crins and Ball, 1989; Robertson, 1984). In a recent study of the *Carex flava* complex, Crins and Ball (1989) reduced it to the rank of variety under *Carex viridula* Michx. ssp. *brachyrrhyncha* (Celakovsky) B. Schmid. Further work is required to improve our understanding of this taxon,

and it may prove to be a local ecotype (Ball, pers. comm.; Crins, pers. comm.).

**Euphrasia salisburgensis** Funk var. **hibernica** Pugsl.

The distribution of this species is confined almost entirely to Ireland, except for a single North American locality, the justification of which rests solely on specimens from Daniel's Harbour, St. Barbe South Distr., collected in 1861 by J. Richardson (CAN). In their treatment of this genus, Sell and Yeo (1970) expressed some misgivings about the origin of the specimen.

**Juncus ambiguus** Guss

In Newfoundland, this coastal halophyte has been known as *Juncus bufonius* L. var. *halophilus* Fern. & Buch. In their treatment of the *J. bufonius* aggregate, Cope and Stace (1978) treated this variety as conspecific with *J. ambiguus,* a distinct species occurring in coastal and brackish habitats throughout Europe, North Africa, Asia and North America.

**Listera** ×**veltmanii** Case

Catling (map, 1976) reported this rare hybrid at sporadic localities from Lake Superior to Newfoundland. The three widely separated stations on the Island are the only records.

**Potentilla bipinnatifida** Dougl. *ex* Hook.

This octoploid member of the *P. pensylvanica* complex was mapped by Kohli and Packer (1976) as occurring in Newfoundland. The reference collections cited were those of Waghorne, made in 1895 from the Bay of Islands. These specimens, and other collections of what is presumably the same taxon from elsewhere in western Newfoundland (St. Barbe North, St. Barbe South, Humber West, White Bay North), have been recorded in the flora as *P. pectinata* Raf. (*nom. illeg.*), or more recently as *P. pensylvanica* L. var. *litoralis* (Rydb.) Boivin (syn.: *P. pensylvanica* var. *pectinata* (Raf.) Lepage). The latter is an essentially eastern coastal calciphile, occurring erratically westward as far as Lake Athabasca. It is quite distinct from *P. bipinnatifida,* a strictly

western taxon. We adhere to this interpretation as resumed by Boivin (1967–68), and espoused by current authors. The report of *P. bipinnatifida* is unfounded.

**Potamogeton strictifolius** Benn.

This species is primarily of the Great Lakes region, although it extends sporadically as far west as Mackenzie Distr., Northwest Territories (map, Haynes, 1974). In Newfoundland it is known only from alkaline waters on limestone bedrock near Flower's Cove, St. Barbe North Distr. Originally the specimens that Fernald collected served as the type material for the description of *P. longiligulatus* Fern. (Fernald, 1932); these specimens have recently been revised to *P. strictifolius* (Hellquist and Crow, 1986). The Newfoundland population represents a slight disjunction in the range toward the northeast.

**Puccinellia ambigua** Th. Sørens.

As defined by Sørensen (1953), this is an endemic saltmarsh species of the Hudson Bay–James Bay region, and the Gulf of St. Lawrence. The tentative opinion of J. Davis (pers. comm.) is that it represents a variant of the more widespread *P. pumila* (Vasey) Hitchc., perhaps deserving of varietal status. In Newfoundland it has recently been reported from the west coast by Thannheiser (1981, 1984). The specimens were identified by M. Barkworth.

**Sagina nodosa** (L.) Fenzl

In Newfoundland this species has been reported as *S. nodosa sensu lato* (Rouleau, 1978), or with two infraspecific taxa: var. *nodosa* and var. *pubescens* (Besser) Mert. & Koch (Boivin, 1966–67; Scoggan, 1978–79). The monograph of the genus by Crow (1978) has shown that two distinct taxa are in fact present but that a name change is required: *S. nodosa* ssp. *nodosa,* to which var. *pubescens* is relegated as a synonym, and secondly, *S. nodosa* ssp. *borealis* Crow. The former appears to have been introduced from Europe, and is now found on the Atlantic coast from Massachusetts to Newfoundland, while the latter is the native subspecies, widespread on shoreline habitats throughout boreal northeastern North America and northern Europe (Crow, 1978).

**Salix ballii** Dorn

Rouleau (1978) reported *S. myrtillifolia sensu lato* for the Island; however, Dorn (1975) recognized two species in this complex: *S. ballii* (syn.: *S. myrtillifolia* var. *brachypoda* Fern.) and *S. myrtillifolia sensu str.* The latter is a mainly western taxon ranging from Alaska to northern Ontario, with disjunct occurrences eastward in Québec (Gaspé, Anticosti), New Brunswick and northwestern Newfoundland. Only four localities are known for the Island; all are on the Strait of Belle Isle coast. Two of these localities were reported by Dorn and the other two are sites of recent collections by G. Argus. *Salix ballii,* which is also rare in Newfoundland, is more widespread on the limestones of the west coast. Endemic in eastern Canada, it ranges from Hudson Bay (Ontario, Québec) to the Gulf of St. Lawrence (maps, Dorn, 1975).

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RHODORA, Vol. 92, No. 872, pp. 294–296, 1990

# NEW ENGLAND NOTE

# SOME NEW RECORDS FOR NEW ENGLAND AND NEW ENGLAND STATES. II.

RAY ANGELO

These previously unreported records for New England states have come to the attention of the Club's Curator of Vascular Plants in the course of executing his curatorial duties. The first such report appeared in Rhodora 91: 342–344 (1989).

These records are not necessarily the first collections of these species in our region, but are intended to represent the first published evidence of these species in the various states of New England. All records cited here are for specimens that have been accessioned by the Club herbarium (NEBC). Their newness has been determined by making use of the most current floras, checklists and other readily available published sources which are based upon public herbarium records.

I thank Dr. David E. Boufford and Leslie J. Mehrhoff for bringing to my attention some of the records noted here as well as earlier, and for permission to include their own records. I also thank Bruce A. Sorrie and Peter F. Zika for permission to include their records.

**New Records for New England**

*Cerastium pumilum* Curtis [Caryophyllaceae]

Westwood, MA (Norfolk Co.); Bruce A. Sorrie (#862); May 7, 1981; "Dry sandy roadside grass, University Avenue just south of Blue Hill Drive. Several patches." [Also collected from Salem, MA (Essex Co.), B. A. Sorrie (#2837) & S. Higgenbotham (1985); Framingham, MA (Middlesex Co.), B. A. Sorrie (#890) (1981); Dartmouth, MA (Bristol Co.), B. A. Sorrie (#877) (1981); Holyoke, MA (Hampden Co.), B. A. Sorrie (#3817), P. Swain, & C. Caljouw (1987).]

East Lyme, CT (New London Co.); C. B. Graves; May 17, 1901; "Field near Niantic River."

[All of these specimens, originally identified as *Cerastium semidecandrum* L., have been reidentified by R. Angelo (1989).]

*Herniaria hirsuta* L. [Caryophyllaceae]
Weston, MA (Middlesex Co.); David E. Boufford (#23165) & Emily Wood; August 14, 1983; "Case Estates of the Arnold Arboretum. Elevation ca. 65 meters. Weed for at least the past three years at 133 Wellesley Street; growing in relatively hard-packed soil and covering an area of about 1 × 1.5 meters."

*Prunus serrulata* Lindley [Rosaceae]
West Hatfield, MA (Hampshire Co.); Harry E. Ahles (#87815); May 2, 1980; "Mixed woods near junction of Linseed and Rocks Roads."

*Centaurium pulchellum* (Swartz) Druce [Gentianaceae]
East Dorset, VT (Bennington Co.); Harry E. Ahles (#87241); August 9, 1979; "Gravelly roadside, East Dorset on Route 7." [Also collected from Jamaica, VT (Windham Co.), H. E. Ahles (#87408) (1979).]
Lanesborough, MA (Berkshire Co.); Bruce A. Sorrie (#2566), Pamela B. Weatherbee et al.; July 26, 1984; "Common by gravel roadside just east of Route 7, entrance to Brodie Mountain cross-country trails." [Also collected from Otis, MA (Berkshire Co.), B. A. Sorrie (#3298) & P. B. Weatherbee (1985); Richmond, MA (Berkshire Co.), B. A. Sorrie (#3268) & P. B. Weatherbee (1985).]

**New Records for Vermont**

*Chaenomeles japonica* (Thunb.) Lindl. ex Spach [Rosaceae]
Essex, VT (Chittenden Co.); Peter F. Zika (#9004); May 29, 1985; "Naturalized in a ditch, railroad right-of-way, Essex Junction." [This specimen, originally identified as *Pyrus cydonia* L., has been reidentified by R. Angelo (1989).]

**New Records for Massachusetts**

*Sedum sexangulare* L. [Crassulaceae]
Barnstable, MA (Barnstable Co.); Richard J. Eaton (#6379) & Henry K. Svenson; September 12, 1970; "Wood road on Wesselhoeft land. Dry boulder-wall of old cellar-hole." [This specimen, originally identified as *Sedum acre* L., has been reidentified by R. Angelo (1989).]

**New Records for Connecticut**

*Bassia hirsuta* (L.) Aschers. [Chenopodiaceae]
Stonington, CT (New London Co.); Leslie J. Mehrhoff (#3333) & William Linke; September 18, 1980; "Sandy soil with *Phragmites* at Mystic Town Beach."

*Teesdalia nudicaulis* (L.) R.Br. [Cruciferae]
Norwich, CT (New London Co.); Leslie J. Mehrhoff (#11255); May 9, 1985; "Dry sandy 'islands' in Route 12, 0.3 miles north of Mohegan-Pequot Bridge exit. Petals — white." [Also collected from Montville, CT (New London Co.), G. C. Tucker (#3932) (1988).]

NEW ENGLAND BOTANICAL CLUB HERBARIUM
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RHODORA, Vol. 92, No. 872, pp. 297–298, 1990

# BOOK REVIEW

In-Cho Chung. (?Dec.) 1989. *Eastern North America as Seen by a Botanist: Pictorial.* Published by the author in 2 volumes, in an edition of 400 sets, hardbound. I. *The Arctic region,* pp. 1–112, 288 colored illus.; II. *The wooded regions,* pp. [i–viii], 113–419, 854 colored illus. Available from the author, 1308 Laurel Drive, Daytona Beach, Florida 32017, U.S.A. (Vol. I, $32.00, Vol. II, $73.00; Vols. I and II together, direct personal orders, $89.00. Prices include postage).

These volumes are worthy successors to an earlier work in the same format, now regrettably out of print, by the same author (*The Arctic and the Rockies as Seen by a Botanist[:] Pictorial.* 343 pp., 574 colored illus. Seoul, 1984). "The Arctic region" treated in the current books includes the eastern Arctic mostly north of the 75th parallel, with some excursions into northern Alaska, and south to Wyoming and Labrador. Coverage of "The wooded regions" extends from subarctic Labrador along the Appalachians and through the Atlantic Coastal Plain from New Jersey to southern Florida. The author is an experienced botanical taxonomist who for over two decades, as he says, has travelled widely in North America and presents his photographs "for an interpretation of the landscapes, to examine the principal vegetational features, and to show some of the characteristic and interesting plants in these regions."

These are extremely fine picture-books, including 1138 numbered photographs in color, almost all by the author, mostly three to a page, with essentially no formal text except the explanatory and often long captions that accompany the pictures. The photographs include not only some of the best closeups of flowering plants, lichens, and fleshy fungi that I have ever seen, but remarkably clear and sometimes breathtaking views of associated habitats. Of the 285 botanical photographs in the volume on the Arctic, 86 are habitat views, including lakes, mountains, tundra, assorted polygons, sedge meadows, and even a herd of musk-oxen. The captions mention common species in the habitats, and discuss such matters as summer and winter temperatures, snow cover and plant distribution.

The volume on the wooded regions follows the same pattern, i.e. pictures of plants interspersed with those of the habitats, the

arrangement alphabetical, essentially in order of the family names of the plants. Many of the more spectacular flowers of eastern North America have been photographed well before, but perhaps the most remarkable pictures in this volume are those in the interior of forests, which are so disappointing in many published articles and books. Dr. Chung seems to have a real talent in producing the effect of depth in the forest, as well as preserving the detail.

These are not coffee-table books, nor are they primarily manuals of wild flowers, though they could serve in either capacity. They should find a place as reference works for students of plant geography, ecology, and floristics and, especially in the Arctic where a larger proportion of the total flora is illustrated, as useful manuals for identification.

The printing and color reproduction, done in Korea, seem exceptionally good. The books are solidly bound and, in view of the numerous colored plates, not over-priced. In a casual perusal I noticed almost no typographical errors. There is an index to plant species, but one could wish for a similar index to place-names as well. A few of the plant portraits are a bit fuzzy, but this seems a minor defect in an otherwise compelling work.

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T. Richard Fisher. 1989. *The Vascular Flora of Ohio,* Volume Two: *The Dicotyledoneae of Ohio*—Part Three: *Asteraceae.* 280 pp. Ohio State University Press, Columbus, OH 43210. ISBN 0-8142-0446-5. [Price: $65.00 (hardbound)]

Being one of the largest families of flowering plants, the Sunflower family (Asteraceae) is treated here, as in some other large flora projects, in a separate book. The volume at hand, though labelled "Part Three," is really the first portion on the Dicotyledoneae of Ohio that has been completed and published. It was very carefully prepared; I have not found a single typographical error. The author, T. Richard Fisher, is an acknowledged expert on the Asteraceae, especially on the genus *Silphium.* He has traveled and collected extensively in Ohio for many years to map the distribution and record observations on the habitats of the many species that occur in the state. In the preface to this book, he states that the guidelines followed are those established by E. Lucy Braun in 1967 in the preparation of Volume One, *The Monocotyledoneae.* The sequence of tribes follows that of Fernald in the 8th Edition of *Gray's Manual of Botany* (1950). Taxonomy and nomenclature are to a large extent traditional and in many cases somewhat outdated. They also follow either Fernald, or Cronquist in *The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada* (Gleason, 1952). To some degree, Cronquist's modified concepts and updated nomenclature in the volume on Asteraceae for the *Vascular Flora of the Southeastern United States* (1980) have been adopted. In a few instances, perhaps not quite often enough, the author has accepted the taxonomy of recent revisions or monographs, e.g., for *Pityopsis, Chrysopsis,* and *Heterotheca,* that of Semple and collaborators (Semple, 1977; Semple et al., 1980), for *Antennaria* that of Bayer and Stebbins (1982), and for *Megalodonta* that of M. L. Roberts (1985).

Seventy-five genera and 276 species of Asteraceae are represented in the Ohio flora, and approximately two-thirds of the species are indigenous. An elaborate family description at the beginning of the text introduces the layperson and the uninitiated botanist to the specialized terminology that applies to members of the Asteraceae. Detailed diagrams of the parts of a capitulum

(head), of the two kinds of florets, and of various pappus types offer further support. This introduction is essential for the lay-person because, regrettably, no glossary of terms is provided. Two sets of keys are available for the identification of the genera, one leading first to one of the ten tribes of Asteraceae represented in Ohio, followed in the appropriate place in the text by a key to the genera in that particular tribe. The second set first provides a key to six artificial assemblages of genera, followed immediately by keys for the identification of genera within each of the assemblages. At the end of the generic descriptions, references to recent taxonomic and cytological treatments and to nomenclatural changes are cited. A complete list of the cited literature can be found preceding the index at the end of the text.

The author points out that the species descriptions deal with Ohio plants only and may be inadequate for the identification of the same species in some other "political" area. Indigenous species are distinguished from introduced weedy taxa or those that are escaped from cultivation by boldfacing of the names. The names of all non-indigenous species are printed in SMALL CAPITALS; one cannot immediately tell whether the plants originated in other continents, or whether they are native in North America but merely adventive or escaped in Ohio. Region of origin is generally indicated for plants introduced from foreign parts of the world, rarely also for adventive plants. Regrettably, however, no statement is made on the overall geographic distribution of species native to North America. In my opinion, such information would have considerably increased the usefulness of this work to botanists outside of Ohio. On the plus side, carefully documented dot maps show the Ohio distribution at the county level for all species that are native and naturalized in the state, including also several adventive species.

Common names are provided if available, also statements about abundance and flowering periods. The reader will appreciate the many comments on personal observations, such as the one on hybridization in *Helianthus*. Many synonyms are cited, especially for those taxa for which the nomenclature differs from that in the works of Fernald or Cronquist. The inclusion of some additional synonyms perhaps would have been helpful to the non-expert who is attempting to sort out the nomenclature when consulting recently published checklists, dictionaries (e.g., *Hortus Third*), treatments on ecology, or floras of other regions.

Among minor errors I noted the following: misplacement of a synonym under *Eupatorium altissimum*; the latter is not the basionym for *Ageratina altissima* (L.) King & Robinson. Instead, the name was based on *Ageratum altissimum* L., which is a synonym of *Eupatorium rugosum*. To comply with the Rules of Nomenclature, *Boltonia asteroides* needs the parenthetical authority "L." In some genera (for instance in *Aster* and *Solidago*), when names are attributed to Muhlenberg, they should correctly be cited as "Muhl. ex Willd."

Illustrations are provided for all of the species described; they were mostly prepared by Sharon Ames Glett. Those of *Solidago* species were drawn by Ellen Powell. Generally the drawings are very good, and it is usually possible to recognize the species they represent. I am afraid, however, that the numbers (or fractions) indicating magnification (i.e., reduction from normal living size) are mostly incorrect. A cursory comparison with herbarium specimens of several species suggests that the numbers are too large by a factor of ca. 2, and that the drawings were reduced in print much more than was anticipated by the artists. Furthermore, the reproduction is not of uniform quality; the printouts of several drawings are a bit faint.

In spite of my criticisms, I regard the book as a very solid, comprehensive, and useful treatment of the Asteraceae of Ohio, a good acquisition for the library of any botanist or amateur interested in the flora of the eastern United States.

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## HESLER VISITING PROFESSORSHIPS IN FLORISTIC BOTANY AT THE UNIVERSITY OF TENNESSEE, KNOXVILLE

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